

## Taxonomic Studies of Podostemaceae of Thailand. 2. Subfamily Tristichoideae and Subfamily Podostemoideae with Ribbon-like Roots

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This paper revises the taxonomy of the species with ribbon-like roots of subfamily Podostemoideae and all species of subfamily Tristichoideae in Thailand. The Tristichoideae comprise *Dalzellia* with four, all new, species (*D. angustissima*, *D. kailarsenii*, *D. ranongensis*, *D. ubonensis*); *Cussetia* (gen. nov.) with *C. diversifolia*, which is transferred from *Dalzellia*, together with *C. carinata* of Cambodia and Laos; and *Terniopsis* with three new species (*T. brevipes*, *T. ramosa*, *T. ubonensis*) and one new record for Thailand (*T. malayana*). *Malaccotristicha* is referable to the emended genus *Terniopsis*. The subfamily Podostemoideae includes *Paracladopus chiangmaiensis* (gen. & sp. nov.), *Cladopus*, with two species, of which *C. fallax* is a new record, and *Polypleurum* with nine species, seven of which and one variety are new (*P. erectum*, *P. longicaule*, *P. longifolium*, *P. longistylusum*, *P. phuwuaense*, *P. rubro-radicans*, *P. wallichii* var. *parvum*, *P. wongprasertii*). A previous paper reported 13 species assigned to three genera of Podostemoideae with crustaceous roots. In total, nine genera and 34 species of Podostemaceae occur in Thailand, indicating that Thailand, like southern India and Sri Lanka, is a center of distribution for the family in Asia.

Key words: *Cladopus*, *Cussetia*, *Dalzellia*, *Malaccotristicha*, *Paracladopus*, Podostemaceae, *Polypleurum*, taxonomy, *Terniopsis*, Thailand.

Most classifications have recognized the family Podostemaceae to include two subfamilies, Podostemoideae and Tristichoideae (Engler 1930, Royen 1951, 1953, 1954, Cook 1996, Rutishauser 1997), while others have recognized two independent families, Podostemaceae sensu stricto and Tristichaceae (Willis 1914, 1915, 1926, Cusset 1973, 1992, Cusset & Cusset 1988). Molecular phylogenies have shown that Podostemaceae sensu lato is a monophyletic family (Les *et al.* 1997, Soltis *et al.* 1999, 2000, Savolainen *et al.* 2000, Kita & Kato 2001, Gustafsson *et al.* 2002). Furthermore, Kita & Kato (2001) showed paraphyly of subfamily Tristichoideae and support for Engler's (1930) classification in which Podo-

stemaceae is divided into three subfamilies, Podostemoideae, Tristichoideae, and Weddellinoideae, as Jäger-Zürn (1997) and Rutishauser (1997) implied from embryological, floral, and vegetative morphology.

Previous comprehensive classifications of Asian Podostemaceae recognized two genera and two species of Tristichoideae (Tristichaceae in those treatments), and five genera and eight species of Podostemoideae (Podostemaceae), with seven genera and 10 species in Thailand (Table 1; Cusset 1973, 1992, Cusset & Cusset 1988). Kato (2004) recently recorded 13 species assigned to *Hydrobryum* and two other crustaceous-rooted genera of subfamily Podostemoideae from Thailand. The lat-

ter genera include two species of *Hanseniella*, *Thawatchaia trilobata* M. Kato, Koi & Y. Kita, and 10 species of *Hydrobryum*. The present paper deals with the rest of the Podostemaceae, *i.e.*, subfamily Podostemoideae with ribbon-like roots and subfamily Tristichioideae. For those taxa of Podostemaceae, Cusset & Cusset (1988) and Cusset (1992) recorded *Cladopus taiensis*, *Polypleurum wallichii* and *P. schmidtianum* of Podostemoideae with subcylindrical or ribbon-like roots and *Dalzellia diversifolia* of Tristichioideae. Cusset & Cusset (1988) also cited a specimen (*Kerr 11985*) of *Malaccotristicha malayana* from peninsular Thailand, but did not mention its taxonomy and distribution in their treatment of the genus *Malaccotristicha*.

By using the materials and methods described by Kato (2004) and additional materials collected in February and December, 2005 and January, 2006, I reexamined those genera and species with the result that three genera and nine species in the Tristichioideae and three genera and 12 species in the Podostemoideae are recognized. Some other specimens remain to be examined. The specimens cited below for each species without indication of herbarium are located in BKF, TI and TNS, and the other examined specimens that are housed in the other herbaria are given their herbarium abbreviations.

## Distribution

From the results of this study and from those of Kato (2004), I recognize a total of nine genera and 34 species of Podostemaceae in Thailand (Table 1). The number of species is apparently much larger than the number (20 spp. or perhaps more) in southern Asia (Sri Lanka and southern India), indicating that Thailand is one of two major distribution centers for Podostemaceae in Asia. However, from the results of our recent field surveys, it would not be surprising to find additional species in Thailand during future research. The Podostemaceae of

TABLE 1. Comparison of classifications of Podostemaceae of Thailand. Dashes indicate the absence of records of corresponding species from Thailand. Numbers in parentheses following species accord with those in Fig. 1.

Cusset (1973, 1992) and Cusset & Cusset (1988)	Kato (2004) and present study
TRISTICHACEAE	TRISTICHOIDEAE
<i>Dalzellia diversifolia</i> (p.p.)	<i>Cussetia diversifolia</i> (5)
—	<i>Dalzellia angustissima</i> (4)
—	<i>Dalzellia kailarsenii</i> (3)
—	<i>Dalzellia ranongensis</i> (2)
—	<i>Dalzellia ubonensis</i> (1)
—	<i>Terniopsis brevis</i> (8)
<i>Malaccotristicha malayana</i>	<i>Terniopsis malayana</i> (6)
<i>Dalzellia diversifolia</i> (p.p.)	<i>Terniopsis ramosa</i> (9)
—	<i>Terniopsis ubonensis</i> (7)
PODOSTEMACEAE	PODOSTEMOIDEAE
—	<i>Cladopus fallax</i> (12)
<i>Cladopus taiensis</i>	<i>Cladopus taiensis</i> (11)
<i>Hanseniella heterophylla</i> (p.p.)	<i>Hanseniella heterophylla</i> (22)
<i>Hanseniella heterophylla</i> (p.p.)	<i>Hanseniella smitinandii</i> (23)
<i>Hydrobryum bifoliatum</i>	<i>Hydrobryum bifoliatum</i> (25)
—	<i>Hydrobryum Chiangmaiense</i> (31)
<i>Hydrobryum griffithii</i>	<i>Hydrobryum griffithii</i> (28)
<i>Hydrobryum japonicum</i>	<i>Hydrobryum japonicum</i> (32)
—	<i>Hydrobryum loeicum</i> (29)
—	<i>Hydrobryum kaengsophense</i> (26)
—	<i>Hydrobryum khaoyaiense</i> (33)
<i>Synstylis micranthera</i>	<i>Hydrobryum micrantherum</i> var. <i>micrantherum</i> (34a)
—	<i>Hydrobryum micrantherum</i> var. <i>crassum</i> (34b)
—	<i>Hydrobryum somranii</i> (30)
—	<i>Hydrobryum tardhuangense</i> (27)
—	<i>Paracladopus Chiangmaiensis</i> (10)
—	<i>Polypleurum erectum</i> (20)
—	<i>Polypleurum longicaule</i> (21)
—	<i>Polypleurum longifolium</i> (17)
—	<i>Polypleurum longistylusum</i> (15)
—	<i>Polypleurum phuwaense</i> (18)
—	<i>Polypleurum rubroradicans</i> (19)
<i>Polypleurum schmidtianum</i>	<i>Polypleurum schmidtianum</i> (14)
<i>Polypleurum wallichii</i>	<i>Polypleurum wallichii</i> var. <i>wallichii</i> (13a)
—	<i>Polypleurum wallichii</i> var. <i>parvum</i> (13b)
—	<i>Polypleurum wongprasertii</i> (16)
—	<i>Thawatchaia trilobata</i> (24)

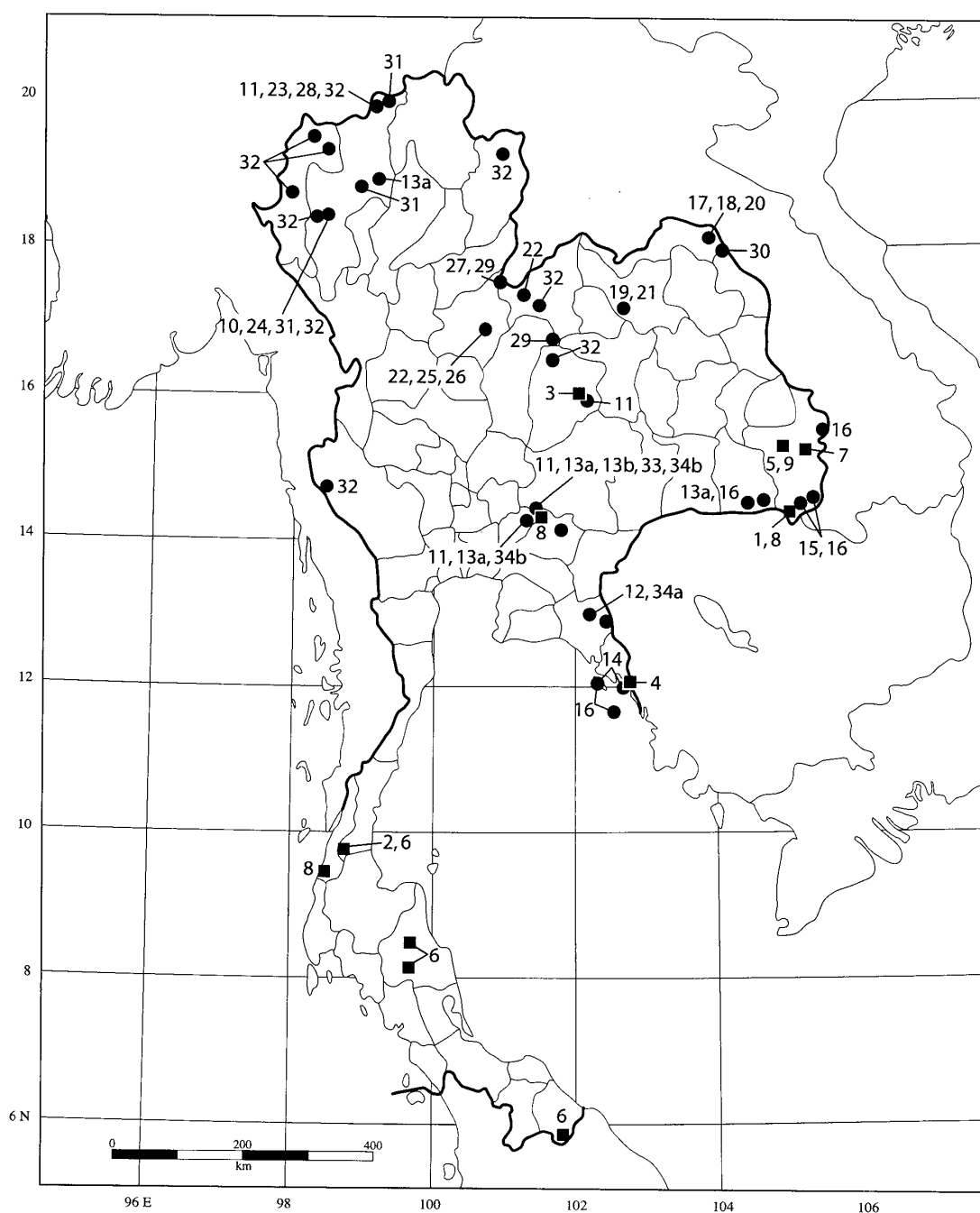


FIG. 1. Map showing distribution of Podostemaceae in Thailand, based on specimens examined. Solid squares and circles indicate Tristichioideae and Podostemoideae, respectively. Numbers for solid circles are the same as those shown in Table 1 and are the species numbers given in the key and enumeration. Circles without numbers indicate unidentified species. 1, *Dalzellia ubonensis*; 2, *Dalzellia ranongensis*; 3, *Dalzellia kailarsenii*; 4, *Dalzellia angustissima*; 5, *Cussetia diversifolia*; 6, *Terniopsis malayana*; 7, *Terniopsis ubonensis*; 8, *Terniopsis brevis*; 9, *Terniopsis ramosa*; 10, *Paracladopus chiangmaiensis*; 11, *Cladopus taiensis*; 12, *Cladopus fallax*; 13a, *Polypleurum wallichii* var. *wallichii*; 13b, *Polypleurum wallichii* var. *parvum*; 14, *Polypleurum schmidtianum*; 15, *Polypleurum longistylusum*; 16, *Polypleurum wongprasertii*; 17, *Polypleurum longifolium*; 18, *Polypleurum phuwaense*; 19, *Polypleurum rubroradicans*; 20, *Polypleurum erectum*; 21, *Polypleurum longicaule*; 22, *Hanseniella heterophylla* (=1, Kato 2004); 23, *Hanseniella smitinandii* (=2, Kato 2004); 24, *Thawatchaia trilobata* (=3, Kato 2004); 25, *Hydrobryum bifoliatum* (=4, Kato 2004); 26, *Hydrobryum kaengsophense* (=5, Kato 2004); 27, *Hydrobryum tardhuangense* (=6, Kato 2004); 28, *Hydrobryum griffithii* (=7, Kato 2004); 29, *Hydrobryum loeicum* (=8, Kato 2004); 30, *Hydrobryum somranii* (=9, Kato 2004); 31, *Hydrobryum chiangmaiense* (=10, Kato 2004); 32, *Hydrobryum japonicum* (=11, Kato 2004); 33, *Hydrobryum khaoyaiense* (=12, Kato 2004); 34a, *Hydrobryum micrantherum* var. *micrantherum* (=13a, Kato 2004); 34b, *Hydrobryum micrantherum* var. *crassum* (=13b, Kato 2004). The detailed locality of Ubon (5, 9) is uncertain.

Thailand are distributed throughout the country, particularly in mountainous regions with rapids and waterfalls, which are suitable environments for these aquatic plants (Fig. 1).

High diversity is also recognizable at the generic level. Among the five genera of subfamily Tristichoideae, *Cussetia* (gen. nov.) is endemic to Southeast Asia (Thailand, Laos, Vietnam). Although *Dalzellia* (exclusive of species referable to *Cussetia*) has been considered to occur only in southern India and Sri Lanka (e.g., Willis 1902a, b, Mathew & Satheesh 1997, Mathew *et al.* 2001), four species occur in Thailand. *Malaccotristicha* has been regarded as a genus endemic to peninsular Malaysia (Cusset & Cusset 1988); it is reduced below to a synonym of *Terniopsis* originally based on a Chinese

species. The emended genus *Terniopsis* consists of six species, *i.e.*, four in peninsular, central and eastern Thailand (one of which extends south to peninsular Malaysia), *T. sessilis* H. C. Chao in central-eastern China, and *T. australis* (C. Cusset & G. Cusset) M. Kato (comb. nov., see Appendix) in a few spots in the northern part of Northern Territory and Western Australia, Australia (Kato *et al.* 2003). The two extra-Southeast Asian species of *Terniopsis* are not basal in a phylogenetic tree (Kita & Kato 2001, Kato *et al.* 2003, Y. Kita unpubl. results). The remaining genus *Indotristicha* with *I. ramosissima* (Wight) P. Royen and *I. tirunelveliana* Sharma, Karthik. & Shetty occurs in southern India. Deduced phylogenetic relationships indicate that the first divergence occurred between a clade of *Terniopsis*

### KEY TO SPECIES OF THAILAND

1. Shoot adhering to rock surface (root absent), crustaceous or broadly ribbon-like, leafy on dorsal surface and at margin; flower bud covered by leafy cupule; flower 3-merous (subfam. Tristichoideae; *Dalzellia*) ..... 2
2. Shoot 3-10 mm wide or wider; dorsal leaves arranged in branched longitudinal rows; peduncle 5-8 mm long, 2.5-4 times as long as ovary ..... 3
3. Dorsal leaves dense, fimbriate; lateral leaves narrowly deltoid, to 1.5 mm long; ovules ca. 30 per locule ..... 1. *Dalzellia ubonensis*
3. Dorsal leaves sparse, separate; lateral leaves deltoid-lanceolate, to 2 mm long; ovules 50-60 per locule ..... 2. *Dalzellia ranongensis*
2. Shoot to 2.5 mm wide; dorsal leaves in 1-2 inconspicuous rows; peduncle 1.5-4 mm long, 1-2 times as long as ovary ..... 4
4. Shoots 1.5-2.5 mm wide; peduncle 1.5-2 mm long; ovary 1.5-2 mm long; ovules 50-60 per locule ..... 3. *Dalzellia kailarsenii*
4. Shoots 1-1.5 mm wide; peduncle 2-7 mm long; ovary 1.3-1.5 mm; ovules 30-50 per locule ..... 4. *Dalzellia angustissima*
1. Root adhering to rock surface, flattened, subcylindrical or ribbon-like; leafy cupule absent, flower bud instead embraced by bracts or leaf-like bracts; flower 2- or 3-merous ..... 5
5. Leaf deltoid or oblong, univeined; flower bud naked (not covered by spathella); flower 3-merous with tepal lobes; ovary locules and stigmas 3, stamens 2 or 3 (subfam. Tristichoideae; *Cussetia*, *Terniopsis*) ..... 6
6. Reproductive shoot complex comprising 3 branches, middle vegetative, 2 laterals floriferous; flowering shoot 4-5 mm long (including leaves) with leaves below flower (comparable to bracts)

- many, in 6 ranks, carinate ..... 5. *Cussetia diversifolia*
6. Reproductive shoot complex comprising 1 floriferous and 1 to few vegetative branches (if plural, floriferous shoot medial); flowering shoot with 2 or several bracts ..... 7
7. Shoot to 2 cm long, composed of ramuli with tristichous imbricate leaves, proximal part of shoot a few times branched; bracts 2 ..... 8
8. Root 0.8-10 mm wide; ramulus 3-90 mm long, often branched; flower-associated short shoots (ramuli) 2 or more; stamens 2 or 3; ovary 1.5-2 mm long ..... 9
9. Root 0.8-1.5 mm wide; ramulus 3-20(-30) mm long; peduncle 2-4 mm long; stamen 2-4 mm long; ovules 25-35 per locule ..... 6. *Terniopsis malayana*
9. Root 2-10 mm wide; ramulus 3-90 mm long; peduncle 7-15 mm long; stamen 5-6 mm long; ovules 8-12 per locule ..... 7. *Terniopsis ubonensis*
8. Root 0.2-1 mm wide; ramulus 2.2-3.5 mm long, simple or rarely forked; flower-associated short shoot (ramulus) single; stamens 2; ovary 1-1.3 mm long; ovules 13-20 per locule ..... 8. *Terniopsis brevis*
7. Shoot to 3 cm long, many times branched, proximal part of shoot 1.5 mm thick, sparsely leafy, distal part comprising ramuli; bracts several ..... 9. *Terniopsis ramosa*
5. Leaves needle-like or ensiform, sometimes sheath-like at base, veins absent or invisible; flower bud covered by globose or ellipsoid spathe; flower 2-merous with tepals separate, linear, 2 on both sides of stamen, stamens 1 or 2 (filament branched); ovary locules (1 or) 2, stigmas 2 (subfam. Podostemoideae) ..... 10
10. Bract 3-4-lobed or digitate; stamen 1; capsule globose, smooth (or weakly striped); capsule valves equal ..... 11
11. Holdfasts present on ventral surface of root under tufts of leaves; tufts of leaves and flowering shoots borne on flanks of root between root branches; bracts linear-oblong, with 2 small lateral basal lobes ..... 10. *Paracladopus chiangmaiensis*
11. Holdfasts absent; tufts of leaves and flowering shoots at root branch points (absent between branches); bracts 3- or 4-lobed or digitate ..... 12
12. Bracts 3- or 4-lobed, lobes thin, semicircular ..... 11. *Cladopus taiensis*
12. Bracts digitate, segments thick, finger-like, obtuse ..... 12. *Cladopus fallax*
10. Bract simple; stamens 1 or 2; capsule ellipsoid, slightly flattened, 8-15-ribbed; capsule valves unequal ..... 13
13. Stamens 2; capsule ribs 8; bract lanceolate or ovate-lanceolate, obtuse or sometimes acute; tufts of leaves on both flanks of root between root branches (13. *Polypleurum wallichii*) ..... 14
14. Root ca. 5 mm wide; leaf to 5(-10) mm long; peduncle 5-8 mm long; ovary to 2.5 mm long ..... 13a. var. *wallichii*
14. Root ca. 3 mm wide; leaf to 2.5 mm long; peduncle to 2-4 mm long; ovary 1.2-1.5 mm long ..... 13b. var. *parvum*
13. Stamen 1; capsule ribs 8-15; upper bract long-acuminate or distally needle-like; tufts of leaves arising on root at branch points or in some species between root branches ..... 15
15. Tufts of leaves borne on flanks of root between branches; capsule ribs 8-12 ..... 16
16. Root 2-4 mm wide; peduncle 6-7 mm long; ovary protruding from spathe at anthesis, 2-locular; stigmas much shorter than ovary; capsule ribs 8 .....

- ..... 14. *Polypleurum schmidtianum*
16. Root 1-1.5 mm wide; peduncle to 1 mm long; ovary enclosed in spathe at anthesis, 1-locular; style plus stigmas as long as ovary or longer; capsule nearly smooth; capsule ribs 10-12 ..... 15. *Polypleurum longistylusum*
15. Tufts of leaves or shoots borne exclusively at points of root branching; capsule ribs 10-15 ..... 17
17. Shoot not prominent (reduced), comprising tufts of leaves; base of leaves embedded in root; flowers always 1 per shoot ..... 18
18. Fresh roots green or dark green, 1.5-3 mm wide ..... 19
19. Bracts 2-4(-6); peduncle 4-7 mm long; spathe 2-3 mm long ..... 20
20. Leaves 5-15 mm long; stigma linear, pointed; ovules ca. 30 per locule, on entire surface of septum ..... 16. *Polypleurum wongprasertii*
20. Leaves 20-40 mm long; stigma subdeltoid; ovules 18-22 per locule, on surface of septum except in lower central area ..... 17. *Polypleurum longifolium*
19. Bracts 4-6; peduncle 10-15 mm long; spathe 4-6 mm long ..... 18. *Polypleurum phuwaense*
18. Fresh roots reddish purple, 3-5 mm wide ..... 19. *Polypleurum rubroradicans*
17. Shoot prominent (tufts of leaves present in juvenile plants); leaves exposed; flowers always or occasionally multiple per shoot ..... 21
21. Root 1-1.5 mm wide; shoot to 5 cm long, simple, erect; leaves 1.5-3 cm long; ovules 15-30 per locule ..... 20. *Polypleurum erectum*
21. Root 2.5-4 mm wide; shoot to 18 cm long, branched, bent at base and floating; leaves 3-7 cm long; ovules 50-70 per locule ..... 21. *Polypleurum longicaule*

and *Malaccotristicha* (which are combined below) and the rest of the subfamily. The latter clade diverged into *Tristicha* and a clade of *Dalzellia* and *Indotristicha* (Kita & Kato 2001, 2004a). It is noted that *Dalzellia gracilis* C. J. Mathew, Jäger-Zürn & Nileena is sister to a subclade of most other species of *Dalzellia* and *Indotristicha* (Y. Kita unpubl. data). *Tristicha* is exceptional in its intercontinental distribution in Africa and America, while all the other genera are distributed in Asia and Australia. Molecular data suggested that subfamily Tristichoideae originated in tropical Asia and subsequently the monotypic Afro-American *Tristicha* migrated to tropical Africa and further to tropical America (Kita & Kato 2001, 2004a).

Concerning subfamily Podostemoideae, two species of *Cladopus* occur in Thailand, while several other species are distributed in the surrounding

southeastern and eastern Asia (the Indian *C. hookerianus* may be excluded from it, as discussed in the Notes under the genus *Cladopus*). It is noteworthy that *Paracladopus chiangmaiensis*, a new genus and species endemic to Thailand, is basal in the *Cladopus* clade. More species (9) of *Polypleurum* occur in Thailand than in South Asia (ca. 7 spp.; Mathew *et al.* 2003). In the monophyletic group comprising the three crustaceous-rooted genera, 8 of ca. 11 species of *Hydrobryum* occur in Thailand, and *Hanseniella* and *Thawatchaia* are endemic to Thailand (Kato 2004; Table 1). It is speculated that Podostemoideae, like Weddellinoideae, diversified in tropical America, followed by migration to tropical Africa and Asia (Kita & Kato 2001, 2004a). The present distribution of *Hydrobryum* likely reflects a past northward expansion and subsequent southward dispersal (Kita & Kato 2004b).

In conclusion, Podostemaceae in Thailand may have been highly diversified subsequent to the primary establishment of Tristichaceae, and secondarily Podostemoideae, in Thailand and neighboring countries.

## Taxonomy

### Subfamily Tristichaceae (Tul.) Engl.

in Engler & Prantl, Nat. Pflanzenfam. 18a: 32, 1830; Rutishauser, Aquat. Bot. 47: 64, 1997; Royen, Meded. Bot. Mus. Herb. Univ. Utrecht 107: 13, 20, 1951, p.p. excl. *Weddellina*; Melchior, Engler's Syllab. Pflanzenfam. 12th ed. 2: 245, 1964, p.p. excl. *Weddellina*; Takhtajan, Div. Classif. Fl. Pl. 269, 1997, p.p. excl. *Weddellina* - Tristichaceae Willis, J. Linn. Soc., Bot. 43: 50, 1914; Cusset, Fl. Cambodge, Laos, Viêt-Nam 14: 75, 1973 - Tristichaceae subfam. Tristichaceae; Cusset & Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., Sect. B, Adansonia 10: 168, 1988. *Typus*: *Tristicha* Du Petit Thouars.

Organ (root or shoot) adhering to rock surface differing between genera. *Cussetia* and *Terniopsis*: root flattened-subcylindrical or ribbon-like, with simple or branched, short shoots (ramuli) on both flanks along length; leaves on ramulus tristichous, univeined, elliptic to deltoid. *Dalzellia*: root absent, shoot crustaceous or broadly ribbon-like, leafy on dorsal surface and at margin; leaf univeined, linear-oblong to deltoid, apex obtuse, more or less dimorphic (dorsal leaf vs. lateral or marginal leaf). Flower solitary (*Dalzellia*) or associated with shoots or ramuli (*Cussetia*, *Terniopsis*), actinomorphic, bud covered by leafy cupule (*Dalzellia*) or by bracts or leaves (*Cussetia*, *Terniopsis*); bracts 2-several or leaves below flower many, tepals tubular, tube 3-lobed, membranaceous; stamens (1 or) 2 or 3 (vs. 1 in *Tristicha* in Africa and America), alternate tepal lobes; ovary locules 3, placentation axile; stigmas 3;

capsule trigonous, 9-ribbed. Genera 5, 3 in Thailand (*Cussetia*, *Dalzellia*, *Terniopsis* [including *Malacotristicha*]).

*Notes*: There is a distinct morphological difference between *Dalzellia* and the rest of the subfamily (*Cussetia*, *Indotristicha*, *Terniopsis*, and *Tristicha*) in that the leading organ is a crustaceous or broadly ribbon-like stem (root lacking) in *Dalzellia*, while such an organ, which bears vegetative and flowering shoots, usually is a root in the latter four genera. The enigmatic Indian *Indotristicha tirunelveliana* is unique in having long holdfasts and "rhizomes" with short leafy vegetative shoots and flowering shoots, and lacking roots (Sharma *et al.* 1974, Uniyal 1999). Mathew *et al.* (2001) regarded *Dalzellia gracilis* as an intermediate linking the two body plans (see Notes under *Dalzellia* below). A preliminary phylogenetic analysis shows that *D. gracilis* is not close to other species of *Dalzellia*, but is sister to the clade of *Dalzellia* and *Indotristicha* (Y. Kita unpubl. data). Further comparative developmental and phylogenetic data on, in particular, *Indotristicha tirunelveliana* and *Dalzellia gracilis* will be useful to understand better the diversity of the Tristichaceae. The different body plans are established at the seedling stage of development (Mohan Ram & Sehgal 1997, Suzuki *et al.* 2002, Imaichi *et al.* 2004, Kita & Kato 2005). The morphological divergence often does not reflect phylogenetic relationships. A molecular phylogeny indicates that saltational evolution perhaps occurred in closely related species, *Dalzellia zeylanica* (Gardner) Wight and Thai congeners with crustaceous, leafy shoots and *Indotristicha ramosissima* with large branched shoots borne on roots (Kita & Kato 2001, Y. Kita unpubl. data).

The floral morphology differs from both Podostemoideae and Weddellinoideae. The flower is 3-merous, consisting of three conspicuous tepals, two or three stamens (rarely one; one in *Tristicha* occurring outside Thailand), three ovary locules

and three stigmas. In the subfamily Podostemoideae it is 2-merous with two reduced tepals, one or two stamens (tepals and stamens many in some American genera), two ovary locules (one in species with reduced ovary septa) and two stigmas. Subfamily Weddellinoideae has five conspicuous tepals, five stamens, two ovary locules and two stigmas.

### **Dalzellia** Wight

Icon. Pl. Ind. Orient. 5(2): 34, 1852 (Jan.); Cusset & Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 10(2): 171, 1988, p.p.; Cook, Aquat. Plant Book, 2nd ed., 185, f. 324, 1996; Mathew & Sathesh, Aquat. Bot. 57: 246, 1997; (non Engler, Nat. Pflanzenfam. 2nd ed. 18a: 32, 1930) - *Terniola* Tul., Arch. Mus. Hist. Nat. Paris 6: 189, 1852 (post Jan.) - *Mniantus* Walpers, Ann. Bot. Syst. 3: 443, 1852 (before Apr.). *Typus*: *Dalzellia zeylanica* (Gardner) Wight.

Root absent. Shoot crustaceous, lobed or broadly flattened and branched, leafy on dorsal surface and at margin; rhizoids on ventral surface. Leaves subdimorphic, univeined; dorsal leaves narrower than marginal (lateral) leaves, arranged in longitudinal, often branched rows, or not in row, facing distal end of crustose shoot; marginal (lateral) leaves facing dorsal leaves. Rosette scattered on surface of old portions of crustose shoot, consisting of many leaves; leaves linear, dense, apparently spiral. Flower bud covered by cupule, cupule with dense reduced leaves; flowers pedunculate, protruding; tepals connate into 3 lobes, copious, membranaceous; stamens 3, alternate tepal lobes; ovary locules 3, placentation axile; stigmas 3; capsule stalked, trigonous, with 9 ribs, dehiscing by 3 valves. Species 6, 4 in Thailand.

*Distribution*: Thailand, Sri Lanka, southern India.

*Notes*: *Dalzellia* consists of six species, *D. zeylanica* of Sri Lanka and southern India, *D. gra-*

*cilis* of southern India, and four, all new species in Thailand. Although Cusset & Cusset (1988) treated *Dalzellia* in a broad sense including *D. diversifolia*, *D. carinata* and *D. sessilis*, they are all excluded here. The former two species are referred to *Cussetia* (gen. nov., described below) and the last to *Terniopsis* (Kita & Kato 2001). The shoot of *D. zeylanica* and *D. ubonensis* is crustaceous at least during young developmental stages, while it is broadly ribbon-like and branched in *D. angustissima*, *D. kailarsenii*, and *D. ranongensis*. *Dalzellia gracilis* is considered to be unusual in the genus in having subcylindrical roots and short, flattened (but neither crustaceous nor broadly-ribbon-like) leafy shoots, and a leafy cupule lacking (Mathew *et al.* 2001). *Dalzellia gracilis* should be excluded from the genus *Dalzellia*, however, and referred to an independent genus (M. Kato unpubl. res.), because phylogenetic analysis shows it to be a sister to the clade of *Dalzellia* and *Indotristicha*, and not close to the other species of *Dalzellia* (Y. Kita unpubl. data).

*Dalzellia* is distinct in Podostemaceae in the markedly flattened shoot with dorsal and lateral leaves (leaves absent on ventral surface of shoot), and the leafy cupules covering the flower buds. The shoot develops by the dorsiventral marginal meristem that divides in a particular way (Imaichi *et al.* 2004). The dorsiventral shoot differs from the cylindrical shoot of *Terniopsis* and *Tristicha*, although the basal portion of the shoot is somewhat flattened in those genera.

*Dalzellia* is widely distributed in southeastern, eastern, northeastern and peninsular Thailand. A molecular phylogenetic study showed that the four species endemic to Thailand are more closely related to each other than to *D. zeylanica*, in accordance with their geographical distances (Y. Kita unpubl. data). It suggests that the four species diverged from a common ancestor, which had diverged from the southern Indian-Sri Lankan *D. zeylanica*.



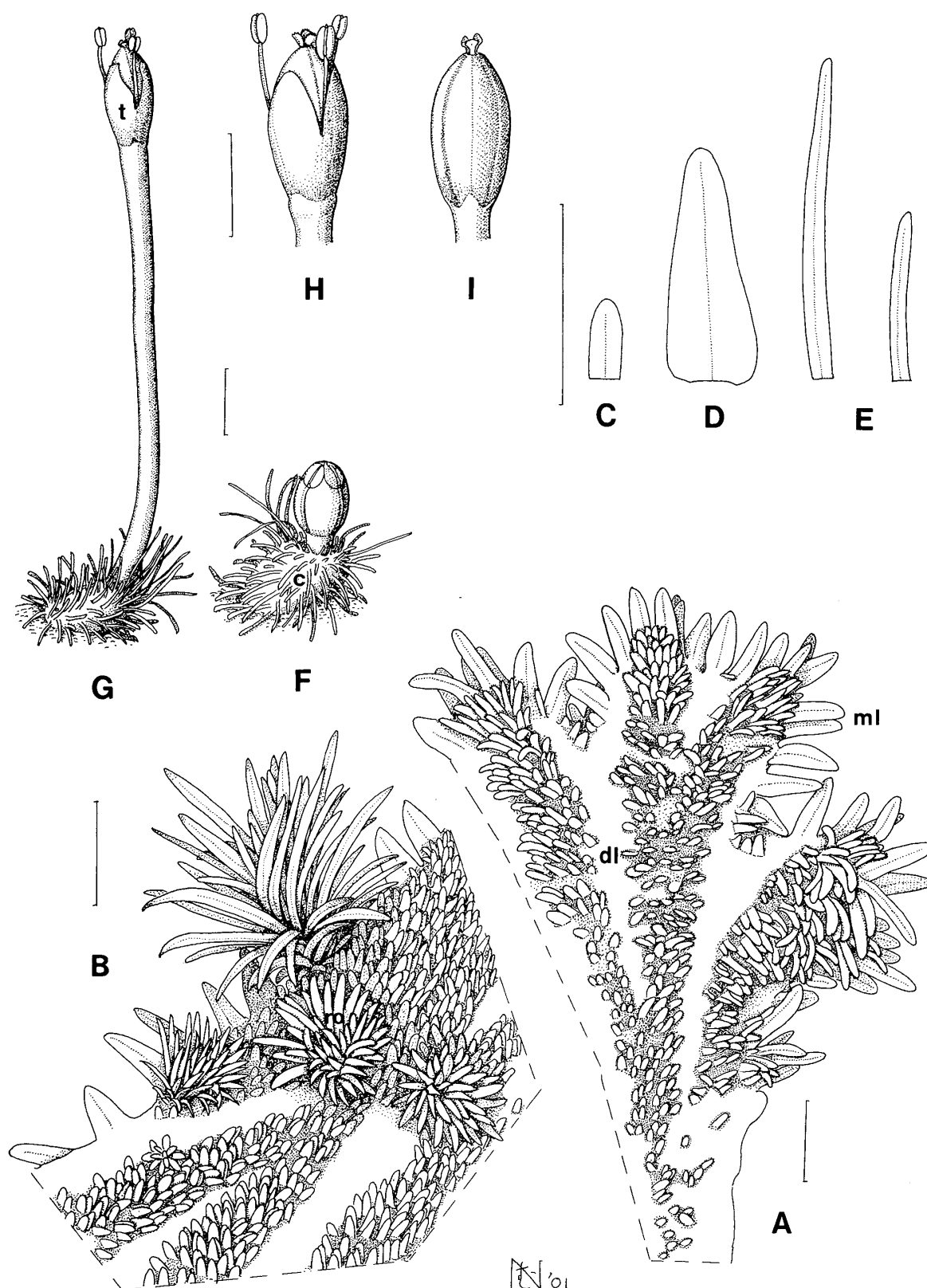


FIG. 2. *Dalzellia ubonensis* (Kato et al. TL-322, type). A, B. Crustaceous shoots with dorsal leaves (dl) in branched rows and marginal leaves (ml). Rosettes (ro) are seen in B. C. Dorsal leaf. D. Marginal leaf. E. Rosette leaves. F. Young flower extruding from leafy cupule (c). Stamens and ovary are visible through tepals in fixed material. G. Flower terminating peduncle. t, tepal. H. Flower at anthesis. I. Fruit. Scales bars = 1 mm.

**1. *Dalzellia ubonensis* M. Kato, sp. nov.** (Fig. 2)

A *D. zeylanicae* foliis dorsalis oblongis, foliis lateralis anguste triangularis, cupulis minoris (usque 1.5 mm latis), a *D. ranongensi* et *D. kailarsenii* foliis dorsalis densis perdurantibus, foliis marginalibus anguste deltoideis, a *D. angustissimae* caulis latissimatibus differt.

*Typus*: Kaeng Lamduan stream, Yoddome Wildlife Sanctuary, Ubon Ratchathani, Eastern Thailand, 14°26'N 105°6'E, 150 m alt., Dec. 29, 2000 (fl. fr.), M. Kato, Y. Kita & T. Wongprasert TL-322 (holo BKF; iso TI, TNS).

Shoot adhering to rock surface, crustaceous, 3-20 mm wide or wider, lobed, leafy. Leaves subdimorphic; dorsal leaves arranged in branched longitudinal rows (rows wide, multiple per shoot lobe), densely fimbriate, linear-oblong, apex rounded, smaller than marginal leaves, 0.3-1 mm long, ca. 0.1 mm wide, facing toward distal end of row; marginal (lateral) leaves fimbriate, narrowly deltoid, apex rounded, to 2 mm × 0.5 mm. Rosettes scattered on dorsal surface of shoot; rosette leaves many, linear, apex rounded, ca. 3 mm × 0.2 mm. Flowers scattered on shoots; bud covered by cupule with dense reduced (0.5-1 mm long) leaves, cupule ca. 1.5 mm thick; peduncle 5-8 mm long; calyx of membranaceous tepals, as long as ovary, 1.5-2 mm long, shallowly 3-lobed, lobes subelliptic, calyx more deeply incised at anthesis; stamens 3, to 2.5 mm long, longer than ovary; ovary obovoid-ellipsoid, ca. 2 mm long, ca. 1 mm thick, 3-locular; stigmas 3, obdeltoid or clavate, 0.3 mm long, papillate; placentation axile; ovules roughly 30 per locule; capsule stalked (stalk to 10 mm long), dark brown, ca. 2 mm long, ca. 1 mm thick, trigonous, ribs 9.

*Distribution*: Thailand (eastern).

*Notes*: *Dalzellia ubonensis*, along with the three other species of Thailand described below, differs from *Dalzellia zeylanica* of Sri Lanka and southern India in the smaller cupules (to 1.5 mm thick vs. ca. 2 mm in *D. zeylanica*). *Dalzellia ubo-*

*nensis* distinctly differs from the other three species in its dense, persistent dorsal leaves and narrowly deltoid marginal leaves, and from *D. ranongensis* with similarly broad shoots (more than 3 mm wide) in bearing ca. 30 ovules per locule.

*Other specimen examined*: Eastern: Kaeng Lamduan stream, Yoddome Wildlife Sanctuary, Ubon Ratchathani, 14°26'N 105°6'E, 150 m alt., fl. Fr. Dec., M. Kato et al. TL-320.

**2. *Dalzellia ranongensis* M. Kato, sp. nov.** (Fig. 3)

A *D. zeylanicae* et *D. ubonensi* caulis late taeniformis, ramosis, foliis dorsalis anguste oblongis, sparsis, foliis lateralis lanceolatis, a *D. kailarsenii* foliis dorsalis perdurantibus, pedunculibus longis (5-8 mm), staminibus ovarii longioribus, a *D. angustissimae* caulis latioribus differt.

*Typus*: Huay Namsainue, near Haew Lom waterfalls, Phato, Chumphon, peninsular Thailand, 09°45'N, 98°40'E, 150 m alt., Feb. 24, 2001 (fl. fr.), T. Wongprasert TL-413A (holo BKF; iso TI, TNS).

Shoot adhering to rock surface, broadly ribbon-like, 3-10 mm wide, isotomously or anisotomously branched or lobed, leafy. Leaves subdimorphic; dorsal leaves arranged longitudinal rows (rows multiple per shoot lobe, branched), moderately sparse, caducous on older portion, linear-oblong, to 0.2-0.5(-2) mm long, 0.05-0.1 mm wide; marginal (lateral) leaves fimbriate, deltoid-lanceolate, apex rounded, to 1-1.5(-3) mm long, 0.2-0.3 mm wide, facing dorsal leaves. Rosettes scattered on dorsal surface of old shoot; rosette leaves many, linear, apex obtuse, 1.5-2.5 mm long, 0.1-0.2 mm wide. Flowers scattered on crustaceous shoot; bud covered by cupule with dense reduced leaves, leaves 0.3-0.4 mm long, cupules 1-1.5 mm thick; peduncle to 5-7 mm long; calyx membranaceous, shallowly, then 1/3 or more deeply lobed (lobes 3), as long as ovary, ca. 2 mm long; stamens 3, ca. 3 mm long, longer than ovary; ovary obovoid-ellipsoid, 1.5-2 mm long, ca.

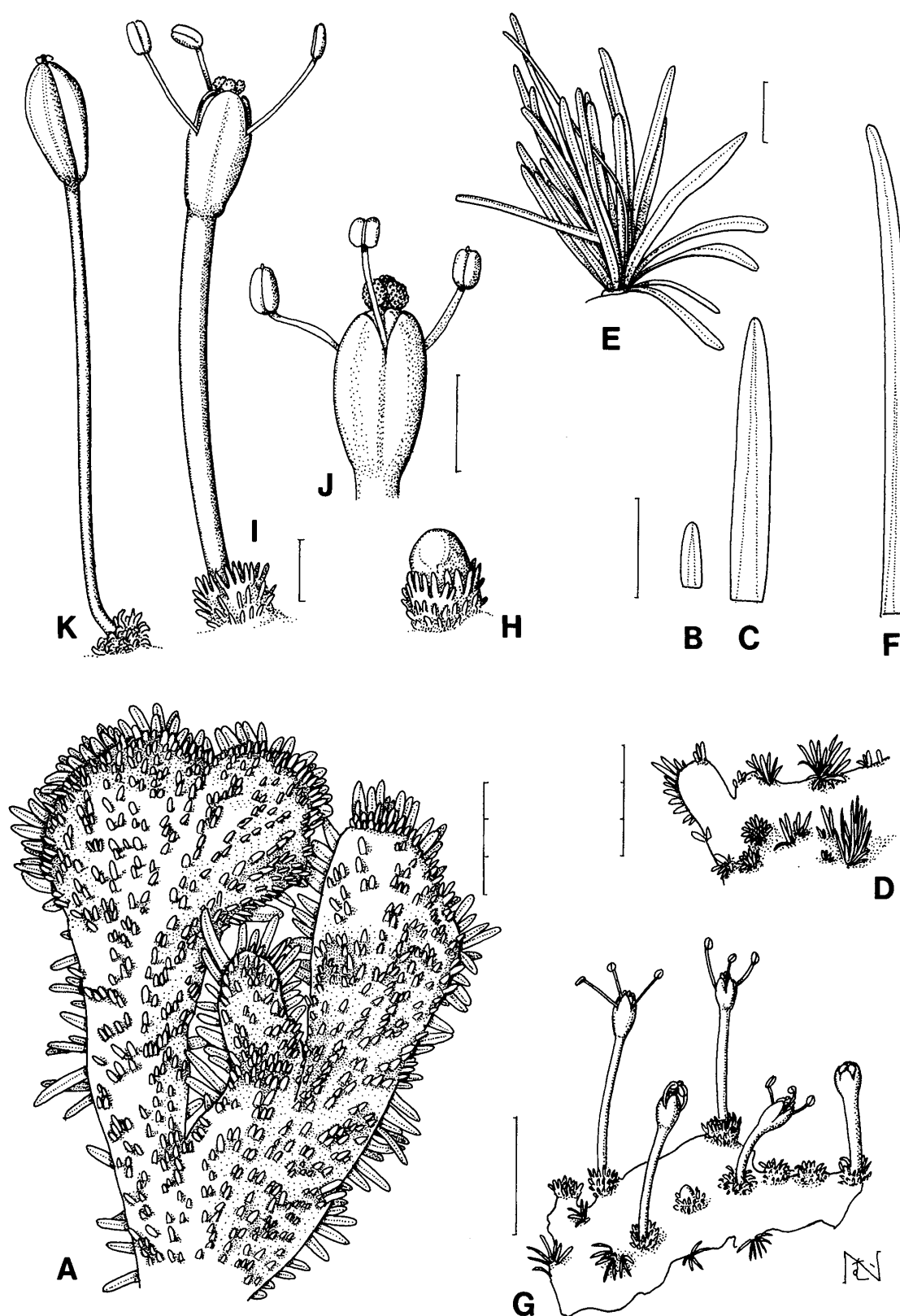


FIG. 3. *Dalzellia ranongensis* (A, M. Kato et al. TL-413; B-K, Wongprasert TL-413A, type). A. Crustaceous shoot with leaves in rows on dorsal surface and at margin. B. Dorsal leaf. C. Marginal leaf. D. Rosettes on old shoot. Dorsal leaves have fallen. E. Rosette. F. Rosette leaf. G. Flowers on shoot. H. Flower bud extruding from leafy cupule. I. Flower at anthesis. J. Magnification of flower. K. Fruit. Scales bars = 3 mm for A, D; 1 mm for B, C, E, F, H-K; 5 mm for G.

1 mm thick, 3-locular, ovules 50-60 per locule, placentation axile; stigmas 3, narrowly ellipsoid, 0.3-0.4 mm long, densely papillate, papillae elongate; capsule stalked (stalk 6-7 mm long), 1.7-2 mm long, 0.8-1 mm thick, trigonous, ribs 9.

*Distribution:* Thailand (peninsular).

*Notes:* *Dalzellia ranongensis* is distinguished from *Dalzellia ubonensis* and *D. zeylanica* with crustaceous shoots by the narrower shoot, moderately sparse, smaller dorsal leaves, and deltoid-lanceolate lateral leaves. *D. ranongensis* is similar to *D. kailarsenii* in bearing 50-60 ovules per locule, but is also distinct from it in the broad, ribbon-like shoot. *Dalzellia ranongensis* has the westernmost distribution in Thailand.

*Other specimen examined:* Peninsular: Huay Namsainue, near Haew Lom waterfalls, Phato, Chumphon, 09°45'N, 98°40'E, 150 m alt., st. Dec., *M. Kato et al.* TL-413. This is an earlier, sterile collection from the same population as the type specimen.

**3. *Dalzellia kailarsenii* M. Kato, sp. nov.** (Fig. 4) A *D. ubonensi* et *D. ranongensi* surculis angustis (usque 2.5 mm latis), taeniis foliorum dorsalium paucis (1-2), foliis dorsalibus longioribus (3-5 mm longis), caducis, pedunculis brevibus (usque 2 mm longis), staminibus longis quam ovariis differt.

*Typus:* Tardtone waterfall, Tardtone Natl. Park, Chaiphaphum, northeastern Thailand, 15°59'N, 102°2'E, 270 m alt., Feb. 12, 2004 (fl. fr.), *M. Kato & T. Wongprasert* TL-1101 (holo BKF; iso TI, TNS).

Shoot adhering to rock surface, broadly ribbon-like, 1.5-2.5 mm wide, isotomously or anisotomously branched, leafy. Leaves subdimorphic; dorsal leaves caducous, arranged in often inconspicuous longitudinal rows (rows 1 or 2 per shoot lobe), fimbriate, linear or oblong, apex semicircular, variable in length, (0.5-)1.5-5 mm long, ca. 0.2 mm wide; marginal (lateral) leaves fimbriate, narrowly deltoid, apex semicircular, 1.5-2.5 mm long, 0.3-0.5 mm wide, facing dorsal leaves. Rosettes scattered on

dorsal surface of old shoots with leaf scars; rosette leaves many, linear, apex obtuse, 2-3 mm long, ca. 0.2 mm wide. Flowers scattered on shoot; bud covered by cupule with dense reduced leaves, leaves 0.3-0.5 mm long, ca. 0.05 mm wide; cupule ca. 1 mm thick; peduncle 1.5-2 mm long, as long as ovary; calyx 3-lobed, membranaceous, initially 1/3 then more deeply lobed, 1.2-1.5 mm long; stamens 3, ca. 2 mm long, as long as ovary, anthers round-ellipsoid, ca. 0.3 mm long, close to stigmas; ovary obovoid-ellipsoid, 1.5-2 mm long, 1-1.2 mm thick, 3-locular, ovules 50-60 per locule, placentation axile; stigmas 3, ovate, 0.3 mm long, papillate; capsule stalked (stalk to 2 mm long), 1.5-2 mm long, ca. 1 mm thick, trigonous, ribs 9.

*Distribution:* Thailand (northeastern).

*Notes:* *Dalzellia kailarsenii* is dedicated to Dr. Kai Larsen, Aarhus University, Denmark, who was the first to collect it (in 1972) from the type locality during his extensive field work for the Flora of Thailand.

*Dalzellia kailarsenii* differs from *D. ubonensis* and *D. ranongensis* in the relatively narrow shoot lobes (to 2.5 mm wide vs. more than 3 mm wide in the latter two species) with 1 or 2 longitudinal rows of dorsal leaves (vs. multiple rows), dorsal leaves long and caducous (3-5 mm vs. usually to 1 mm and caducous only on old shoots), short peduncle (to 2 mm vs. more than 5 mm), and stamens as long as ovary (vs. longer than ovary). It differs from *D. angustissima* in the broader shoot. *D. kailarsenii* has the northernmost distribution.

*Other specimens examined:* Northeastern: Tardtone waterfall, Chaiphaphum, 15°59'N, 102°2'E, 270 m alt., fl. fl.-buds, Dec., *M. Kato et al.* TL-1001; Tard Tone, Chaiphaphum, 300-400 m alt., fr. Feb., *Kai Larsen* 31811, 31812 (AAU).

**4. *Dalzellia angustissima* M. Kato, sp. nov.** (Fig. 5) A *D. ubonensi* et *D. ranongensi* surculis angustis (usque 1-1.5 mm latis) differt, *D. kailarsenii* surculis angustis, staminibus longis quam ovariis similis sed surculis angustior, pedunculis longioribus, ovari-

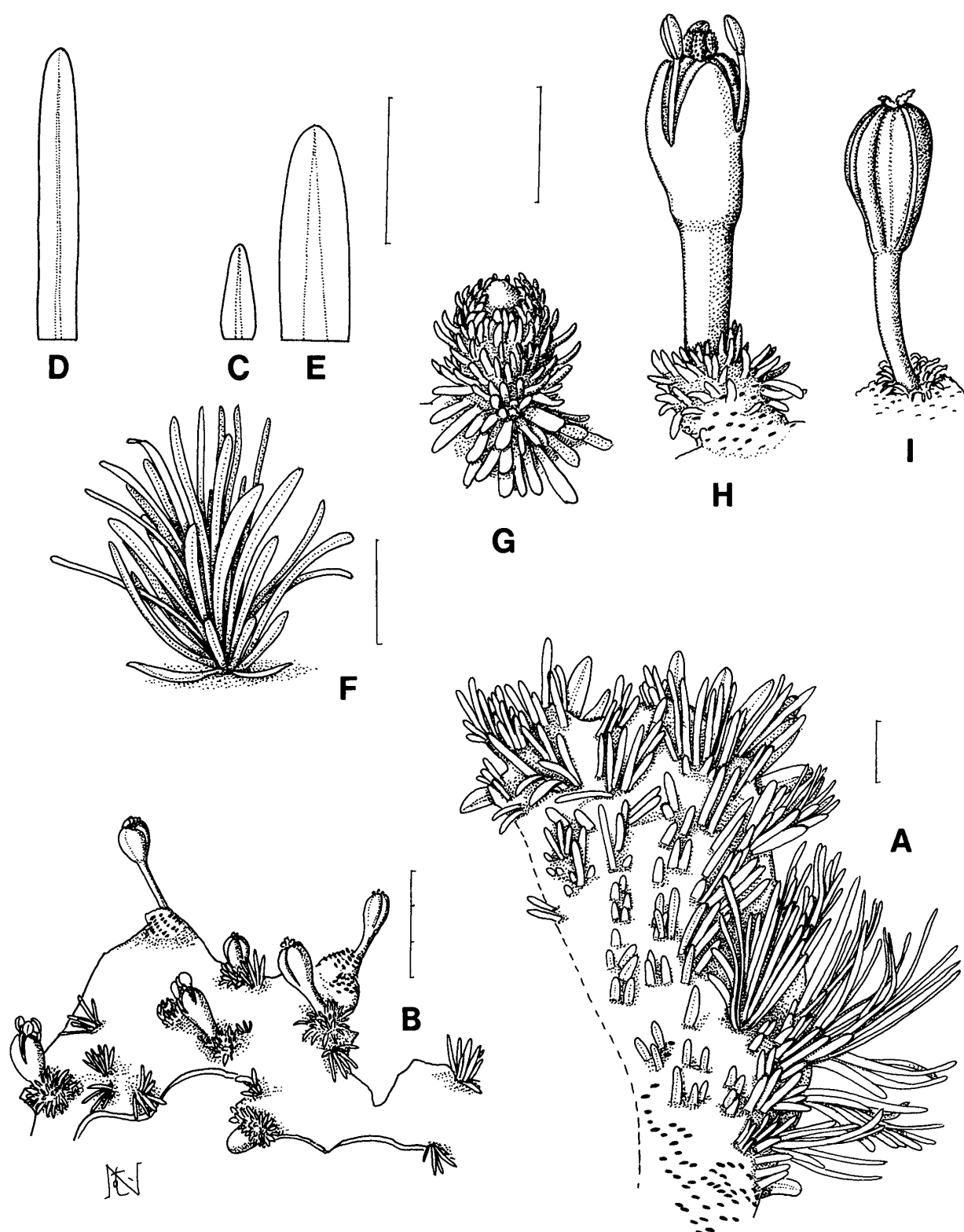


FIG. 4. *Dalzellia kailarsenii* (Kato & T. Wongprasert TL-1101, type). A. Crustaceous shoot with leaves in rows on dorsal surface and at margin. Dorsal leaves on older portion of shoot have fallen leaving leaf scars. B. Old crustaceous shoot with flowers and buds. Rosettes are scattered and all other leaves have fallen. C, D. Short and long dorsal leaves. E. Marginal leaf. F. Rosette. G. Flower bud in leafy cupule. H. Flower at anthesis. Leaf scars are present in lower part of cupule. I. Fruit. Scales bars = 1 mm for A, C-I; 3 mm for B.

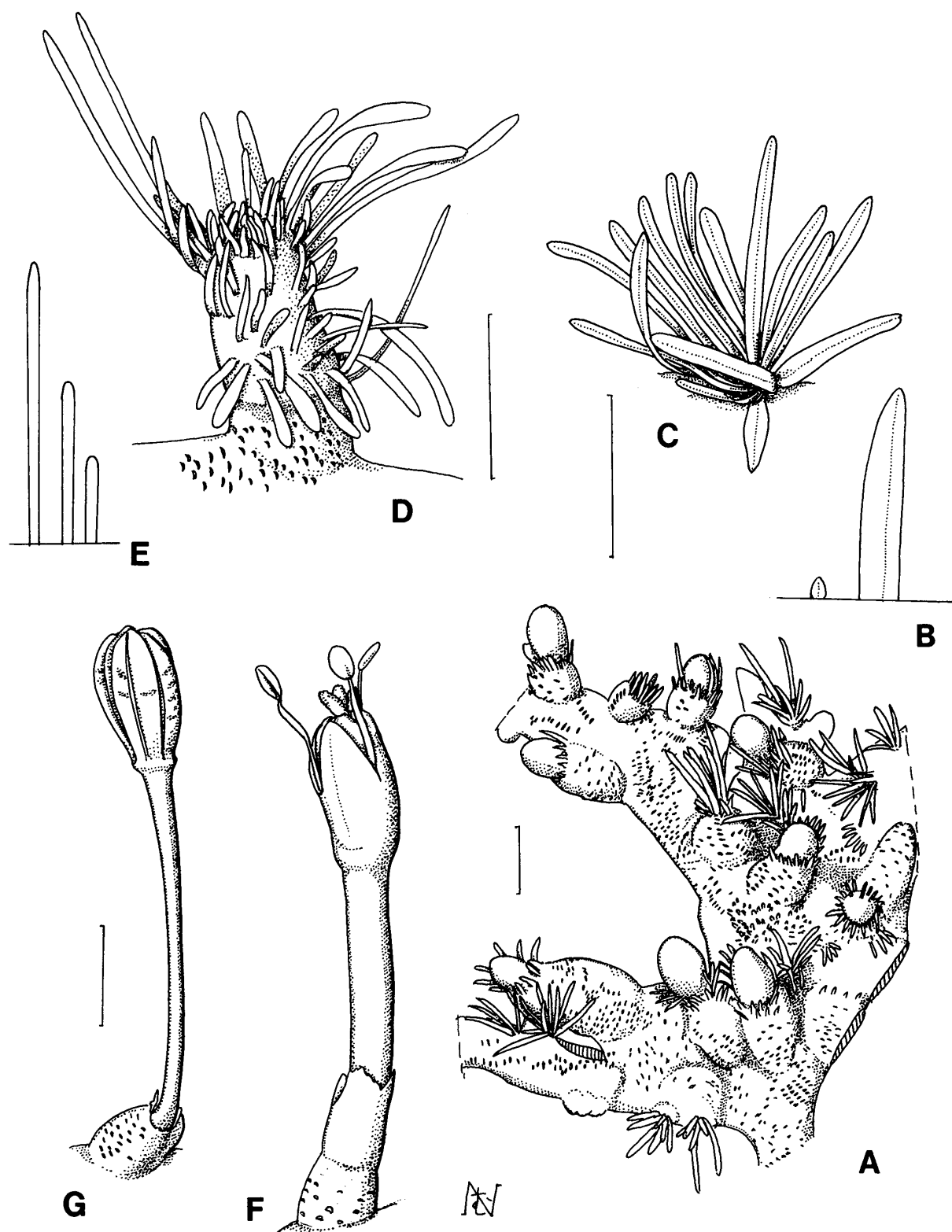


FIG. 5. *Dalzellia angustissima* (Kato et al. TL-1302). A, Ribbon-like shoot with flower buds. Shoot branches on the right overlap. B, Dorsal (left) and marginal leaves (right). C, Rosette. D, Leafy cupule. E, Cupule leaves. F, Flower at anthesis. G, Fruit. Scale bars = 1 mm.

is parvioribus, ovulis paucioribus differt.

*Typus*: Saphanhin waterfalls, Ban Tha Sen, Trat, southeastern Thailand, 12°06'N, 102°43'E, 40 m alt., Jan. 18, 2006 (fl.), M. Kato, S. Koi & T. Wongprasert TL-1507 (holo BKF; iso TI, TNS).

Shoot adhering to rock surface, ribbon-like, 1-1.5(-2) mm wide, frequently isotomously or anisotomously branched, entangled, leafy. Leaves (mostly fallen; further observation using fresh vegetative material is needed) subdimorphic, univeined; dorsal leaves caducous, leaf scars dense on entire dorsal surface of root, linear-oblong, apex semicircular, 1-2 mm long, ca. 0.1-0.2 mm wide; marginal (lateral) leaves fimbriate, narrowly deltoid-oblong, apex semicircular, 1.5-2 mm long, 0.3-0.4 mm wide. Rosettes scattered on shoot; rosette leaves many, univeined, linear, apex obtuse, 1-2 mm long, 0.1-0.2 mm wide. Flowers many, at shoot apex; bud covered by cupule; cupules with dense reduced leaves (leaves 0.3-0.5 mm long, less than 0.1 mm wide, but gradually transitional to dorsal leaves), 1-1.3 mm thick; peduncle 2-7 mm long; calyx membranaceous, 3-lobed, 1/3 length of calyx or often more deeply lobed, 1.2-1.5 mm long; stamens 3, ca. 1.5 mm long, as long as ovary or slightly longer; anthers subround, ca. 0.2-0.3 mm long, close to stigmas; ovary obovoid-ellipsoid, 1.3-1.5 mm long, 0.7-0.9 mm thick, 3-locular, ovules 30-50 per locule, placentation axile; stigmas 3, ovate, 0.3 mm long, papillate; capsule stalked (stalk 4-8 mm long), 1.2-1.8 mm long, 0.6-0.8 mm thick, trigonous, ribs 9.

*Distribution*: Thailand (southeastern).

*Notes*: The shoot of *Dalzellia angustissima* is the narrowest (not crustose but ribbon-like) among the species of *Dalzellia*, and even narrower than the ribbon-like root of some species of *Terniopsis*, *Cladopus* and *Polypleurum*. *Dalzellia angustissima* differs from *D. ubonensis* and *D. ranongensis*, which have crustose shoots 3-20 mm wide, and is the most similar to *D. kailarsenii* in the narrow shoots, the stamens as long as the ovaries and the

anthers close to the stigmas. However, *D. angustissima* differs from *D. kailarsenii* in the shoot being 1-1.5 mm wide vs. 1.5-2.5 mm wide in *D. kailarsenii*, the dorsal leaves dense and not arranged in row, the peduncle longer (2-7 mm vs. 1-5-2 mm long), the ovary smaller (to 1.5 mm vs. 1.5-2 mm long), and the ovules fewer (30-50 vs. 50-60 per locule). The non-crustaceous shoots, like those of *D. kailarsenii*, are reminiscent of the subcylindrical or ribbon-like shoots of other members of Tristichioideae (e.g., *Indotristicha tirunelveliana*, *Dalzellia gracilis*, *Terniopsis australis* and *Tristicha trifaria*). Jäger-Zürn (1995, 2003) interpreted the crustaceous shoot of *D. zeylanica* as a coenosome (Coenosom), in which adjacent shoot units are fused, although their apical meristems are separate. *Dalzellia angustissima* and *D. kailarsenii* are similar to the suggested ancestral form with branched shoots, but phylogenetically they are not basal in the clade of *Dalzellia* (Y. Kita unpubl. data).

*Other specimen examined*: Southeastern: Saphanhin waterfalls, Ban Tha Sen, Trat, 12°06'N, 102°43'E, 40 m alt., fr., M. Kato et al. TL-1302.

### **Cussetia** M. Kato, *gen. nov.*

A *Dalzellia* et *Terniopse* bractis nullis, surculis floriferis longis, bracteis multis, 6-fariatis, carinatis, a *Tristicha* floribus semper 3 staminibus, caulibus sterilibus plerumque simplicibus, ab *Indotristicha* (et *Dalzellia*) cupulis nullis differt.

*Typus*: *Cussetia diversifolia* (Lecomte) M. Kato.

Root creeping, adhering to rock surface, ribbon-like, with many shoots borne on both flanks. Shoots comprising vegetative and floriferous shoots or rarely only floriferous shoots; leaves on vegetative shoot in 3 ranks, one dorsal, two ventral-lateral; leaves (obvious bracts absent) on floriferous shoots 6-ranked, keeled in middle on abaxial surface, coriaceous; flower solitary at shoot apex, pedunculate; calyx with 3 lobes, membranaceous, lobes with

midrib, pale; stamens 3, alternate tepal lobes; ovary locules 3, placentation axile; stigmas 3, separate from each other; capsule stalked, obovoid, trigonous, with 9 ribs, dehiscent by 3 valves. Species 2, 1 in Thailand.

*Distribution.* Thailand, Cambodia, Laos.

*Notes.* Cusset & Cusset (1988) defined the genus *Dalzellia* in a very broad sense, including two species from Southeast Asia, *D.* (= *Cussetia*) *diversifolia* from Thailand and Laos, and *D.* (= *Cussetia*) *carinata* from Cambodia and Laos. The Chinese *Terniopsis* also was treated as congeneric. As a result, the genus is considerably heterogeneous. The present observations, however, along with previous descriptions and illustrations, indicate that these species differ greatly from *Dalzellia* and should be excluded from it. Furthermore, there is confusion in the taxonomy and nomenclature. Because the type specimen of *D. diversifolia* comprises plants of two species, they are transferred to *Cussetia* and *Terniopsis* below. The differences between *Cussetia* and *Dalzellia* (except for the Indian *D. gracilis*; but see Notes under *Dalzellia*) include the ribbon-like root with shoots on both flanks (vs. shoot crustaceous and root lacking in *Dalzellia*), the reproductive shoot bearing keeled leaves (bracts) in 6 ranks and a single terminal flower, one or two flowering shoots associated by one vegetative branch, and the flower bud naked (vs. the flower covered by a leafy cupule).

*Cussetia* is most similar to *Terniopsis*, but differs in having many leaves (bracts) in 6 ranks on the floriferous shoot and an aggregation of one median, long vegetative shoot and one or two lateral flowering shoots. In comparison, in *Terniopsis* the bracts are 2 (to several) and single short shoots are associated with flowering shoots. The phylogenetic relationship of *Cussetia* remains to be determined.

The generic name *Cussetia* is dedicated to C. Cusset and G. Cusset who greatly contributed to the taxonomy and biogeography of the Podostemaceae worldwide.

**5. *Cussetia diversifolia* (Lecomte) M. Kato, *comb. nov.*** (Fig. 6) – *Terniola diversifolia* Lecomte, Not. Syst. 1: 7, 1909, p.p.; Fl. Gén. Indochin. 5: 43, 1926, p.p. – *Lawia diversifolia* (Lecomte) Koidz., in Doi, Fl. Satsum. 1(4): 53, 1929, p.p. – *Dalzellia diversifolia* (Lecomte) C. Cusset, Fl. Cambodge, Laos, Viêt-Nam 14: 78, pl. 12, f. 1-3, 1973, p.p.; Cusset & Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 10(2): 173, 1988, p.p. *Typus:* Ubon Ratchathani, eastern Thailand, anno 1866-1867, C. Thorel 2791 (lecto P!). (This specimen has been mistakenly cited as C. Thorel 2731 [Lecomte 1909, Cusset 1973]. See also typification of *Terniopsis ramosa* below).

Root creeping, adhering to rock surface, ribbon-like, 1-2 mm wide, branched, lobed (holdfasts) at shoot insertions, with many shoots rather closely arranged on both flanks. Shoot aggregations comprising 1 median vegetative shoot with 1 floriferous shoot on each side, or sometimes with 1 vegetative shoot and 1 flowering shoot, rarely with 2 flowering shoots (vegetative shoot undeveloped or hidden), vegetative shoot 5-15 mm long, much longer than flowering shoot (4-5 mm long including leaves); leaves dimorphic, leaves on vegetative shoot in 3 ranks, one dorsal, two ventral-lateral, ovate-lanceolate to oblong-lanceolate, apex obtuse or subacute, thin, 1-1.5 mm × 0.5-0.7 mm, distal leaves gradually smaller and narrower; leaves (bracts) on flowering shoot in 6 ranks, 2 or 3 per rank, deltoid-ovate, apex obtuse, keeled in middle on abaxial surface, 1.5-2.5 mm × 0.5-1 mm, thick, coriaceous; flower 1, at shoot apex; peduncle 3-7 mm long; tepal 1.2-1.4 mm long, lobed 1/3-1/4 to base, lobes 3, membranaceous, univeined, pale; stamens 3, alternate tepal lobes, as long as tepals or longer, anthers deltoid; ovary 3-locular, ellipsoid, apex subtruncate, 1.2-2 mm × 0.7-1 mm long, placentation axile; stigmas 3, separate from each other, multilobed; capsule stalked, obovoid, trigonous, ribs 9.



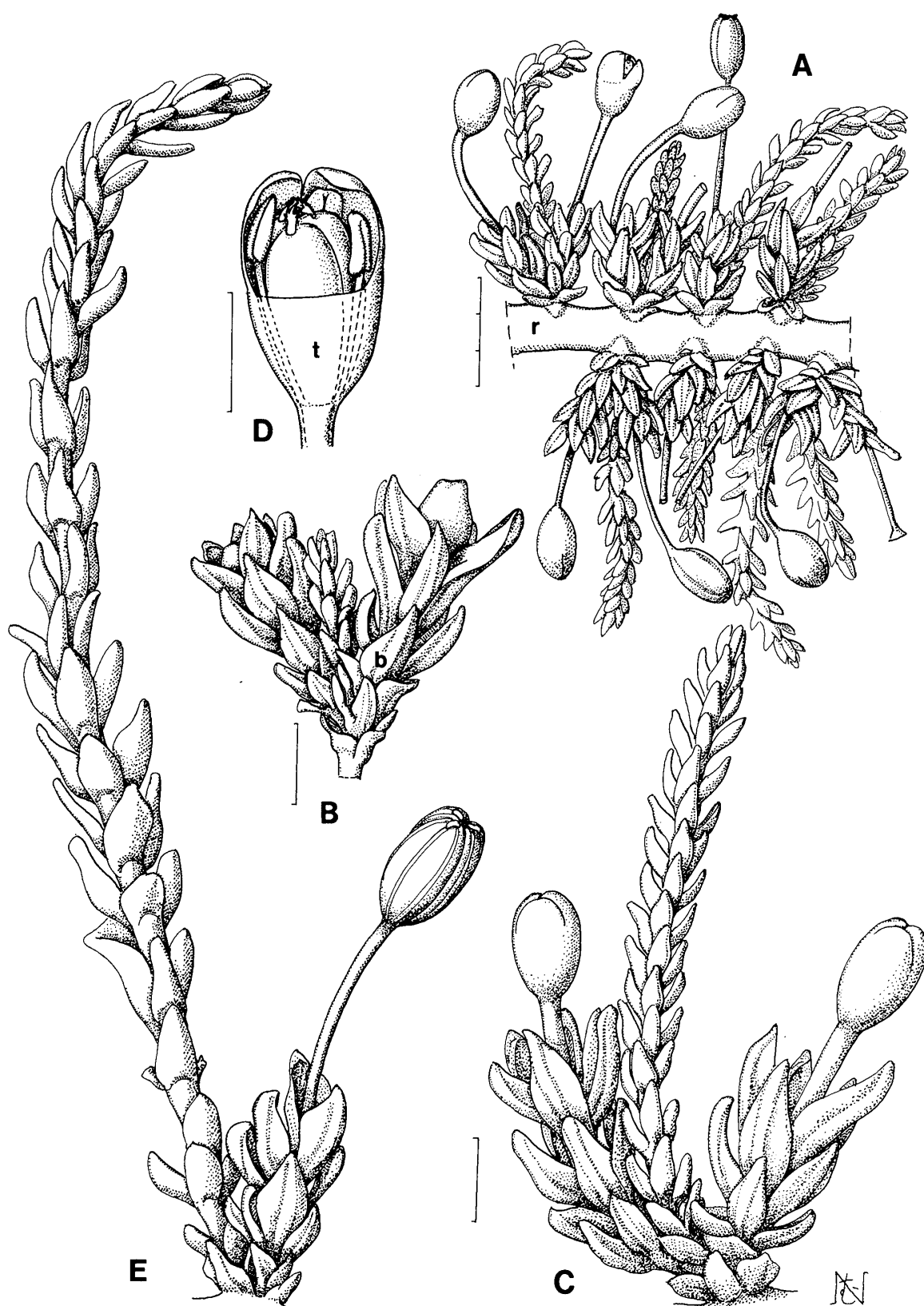


FIG. 6. *Cussetia diversifolia* (C. Thorel 2791 [P], type; herbarium specimen). A. Ribbon-like root (*r*) with shoot complexes along flanks. B. Young shoot complex with middle, still short vegetative shoot and two lateral floriferous shoots with flower buds above bracts (*b*). C. Older complex with flowers not yet open. D. Flower bud with distal part of tepal (*t*) removed. E. Mature complex with one vegetative (left) and one floriferous shoot bearing fruit (right). Scales bars = 3 mm for A; 1 mm for B-E.

*Distribution:* Thailand (eastern).

*Notes:* The type specimen (*C. Thorel 2791*) of *Cussetia diversifolia* is a mixed collection with plants of *Terniopsis ramosa* described below. The original description (Lecomte 1909, 1926) is applicable to both species. The phrase “rhizomate lineari, semi-cylindrato et pennatio-ramuloso,” fits both, and the remaining phrases “ramulis dissimilibus, aliis flores gerentibus, aliis sterilibus. Ramuli floriferi foliis carinatis, ramuli steriles foliis tenuibus instructi” match *C. diversifolia* as redefined here. Furthermore, since the epithet seems to reflect the latter description, I judge that what Lecomte (1909, 1926) intended to describe is the emended *C. diversifolia*. Illustrations by Cusset (1973, pl. 12, f. 1-3) fit this species.

*Cussetia diversifolia* is most similar and closely related to *C. carinata* in the absence of obvious bracts, carinate leaves in 6 ranks on the flowering shoot, and tepal-like, pale filaments. It differs from *C. carinata* in the shoot comprising a middle vegetative and two lateral flowering branches (vs. a vegetative and a flowering branch in *C. carinata*), 2 or 3 leaves per rank on flowering shoots (vs. ca. 8), peduncle to 7 mm (vs. 10-12 mm), and stigmas filamentous, entire (vs. sometimes branched, lobulate).

The non-Thai *Cussetia carinata* is given a formal combination in the Appendix.

### **Terniopsis** C. H. Chao

Contr. Inst. Natl. Acad. Peiping 6: 2, 1948 (publ. 1949); Acad. Bot. Yunnan. 2: 296, 1980; Fl. Fukien 1: 479, 1982; T.-L. Wu, Fl. Reipubl. Popularis Sin. 24: 1, 1988; Kato & Kita, Acta Phytotax. Geobot. 54: 88, 2003. *Typus:* *Terniopsis sessilis* H. C. Chao.

*Malaccotristicha* C. Cusset & G. Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 10(2): 174, 1988; Cook, Aquat. Plant Book, 2nd ed., 185, f. 324, 1996: *syn. nov.* *Typus:* *Malaccotristicha malayana* (J. Dransf. & Whitmore) C. Cusset & G. Cusset.

*Dalzellia* auct. (non Wight); C. Cusset & G. Cusset, Bull. Mus. Natl. Hist. Nat., Adansonia 10(2): 171, 1988, p.p.; Qiu & Philbrick, Fl. China 5: 190, 2003, p.p.

Root ribbon-like, creeping, adhering to rock surface, flattened, branched. Shoots or ramuli (short shoots) on both flanks of root, simple or branched, associated with rudimentary holdfasts; leaves of ramuli in 3 ranks, 1 median, 2 lateral, subdimorphic, apex obtuse. Flowering shoots also borne on both flanks of root, associated with 1-few, short sterile ramuli, bracts 2-several; flower pedunculate; calyx 3-lobed, membranaceous; stamens 2 or 3, alternate tepal lobes; ovary obovoid-ellipsoid, 3-locular, placentation axile; stigmas 3, separate from each other; capsule stalked, trigonous, with 9 ribs, dehiscing by 3 valves. Species 6, 4 in Thailand.

*Distribution:* Thailand, Malaysia, central-eastern China (Fujian), northwestern Australia (Northern Territory).

*Notes:* When describing *Terniopsis* as a new genus from Fujian, central-eastern China, Chao (1948, 1980) considered that the sole species, *T. sessilis*, was most closely related to *Terniola* (= *Dalzellia*). Cusset & Cusset (1988) placed it under *Dalzellia* sensu lato, whose type is the rootless *D. zeylanica* and to which the rooting *T. sessilis*, along with *Cussetia diversifolia* and *C. carinata*, was referred (for treatment of the last two species see *Cussetia* above and the Appendix below). In contrast, Cusset & Cusset (1988) established the new genus *Malaccotristicha* based on *M.* (= *T.*) *malayana* from peninsular Malaysia. *Terniopsis* and *Malaccotristicha* have a sister group relationship (Kita & Kato 2001, Y. Kita unpubl. data) and share flattened subcylindrical roots, adventitious shoots/ramuli on the root, tristichous leaves on the ramuli, single short ramuli associated with single flowers, two bracts subtending a flower, trimerous flowers with 3-lobed tepals, 2 or 3 stamens, three stigmas, and 3-locular ovary. In a taxonomic study

of Chinese Podostemaceae, Kato & Kita (2003) pointed out that, although *Terniopsis* and *Malaccotristicha* are phylogenetically separate, there are only a few small differences, e.g., the ovate vs. triangular leaves and the axile vs. free central placentation (Dransfield & Whitmore 1970). Examination of ample material collected from Thailand, as described below, and herbarium specimens clearly shows that such differences are not detectable between the genera: there is variation in leaf shape among species, and *T.* (= *M.*) *malayana* has the same axile placentation in the 3-locular ovary as the other species. Therefore, generic segregation is untenable and the two genera should be treated as congeneric under the genus *Terniopsis*. In contrast to the high morphological accordance, the two sister groups are separated by considerable DNA sequence differences (Kita & Kato 2001, Y. Kita unpubl. data). In conclusion, I do not propose an infrageneric segregation, but recognize two phylogenetic groups, i.e., the “*Terniopsis*” and “*Malaccotristicha*” groups, which can be recognized only by molecular data.

In Cusset & Cusset's (1988) classification, *Malaccotristicha* was monotypic with *M. malayana* occurring in restricted areas of peninsular Malaysia, but they also cited a specimen from the Isthmus of Siam as *M. malayana*. Our recent field studies resulted in the discovery of *Terniopsis* (= *Malaccotristicha*) in peninsular, central, and eastern Thailand. As a result, *Terniopsis* in Thailand is composed of four species, *T. malayana* on the Malay Peninsula (peninsular Thailand and Malaysia), *T. brevis* in central, eastern and peninsular Thailand, and *T. ramosa* and *T. ubonensis* endemic to eastern Thailand. The first three species, which are closely related to each other, belong to the “*Malaccotristicha*” group, and the last belongs to the “*Terniopsis*” group (Y. Kita unpubl. data). Although *T. sessilis* of the “*Terniopsis*” group, sister to *T. ubonensis*, occurs disjunctly in central-eastern China, both groups are likely to have originated in

southeastern Asia. *Terniopsis* (= *Malaccotristicha*) *australis*, a member of the “*Malaccotristicha*” group, is also disjunct in northwestern Australia and has been commonly recognized as *Tristicha trifaria* (e.g., Aston 1990) or *Tristicha australis* (Cusset & Cusset 1988). A molecular phylogeny and comparative morphology show that it belongs to *Malaccotristicha* (Kato *et al.* 2003) or *Terniopsis* emended (this study; the nomenclatural change of *Terniopsis australis* is provided in the Appendix). Recently, *M. malayana*, the type species of *Malaccotristicha*, was referred to *Tristicha* (Cook & Rutishauser 2001), which, however, results in the genus *Tristicha* being paraphyletic, because *Tristicha* is more closely related to *Dalzellia* and *Indotristicha* than to *Terniopsis* (= *Malaccotristicha*) (Kita & Kato 2001). Consequently, *Terniopsis* is distributed from southeastern and eastern Asia to northwestern Australia. Thailand, with four of the six species, is main distribution region.

Among the genera and species of Tristichaceae with the ramuli borne on the subcylindrical roots and trimerous flowers, *Terniopsis* is distinguished from *Cussetia* by the two bracts (several in *M. ramosa*) and single to few reduced shoots (ramuli) associated with the flower (see Notes under *Cussetia* above). *Tristicha* is an Afro-American genus unique in having capless roots and single stamens.

During examination of herbarium specimens I encountered two specimens, Vidal 947 (P), 12.1. 1941, Muong Phalan, Laos, and Harmand s. n. in Pierre 2313, p.p. (P), Bassac, Laos. They are tentatively identified as *Terniopsis*, based on two or a few membranaceous bracts and tristichous leaves on the flower-associated ramuli. If the identification is correct, the genus is more widely distributed in Southeast Asia than we are aware.

**6. *Terniopsis malayana*** (J. Dransf. & Whitmore) M. Kato, **comb. nov.** (Fig. 7) – *Indotristicha malayana* J. Dransf. & Whitmore, Blumea 18: 154,

pl. 1, f. 1, 1970; Steenis, Fl. Males. I, 6(6): 964, f. 12, 1972 - *Malaccotristicha malayana* (J.Dransf. & Whitmore) C.Cusset & G.Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 10(2): 174, 1988 - *Tristicha malayana* (J.Dransf. & Whitmore) C.D.K.Cook & Rutish., Taxon 50: 1166, 2001. *Typus*: Malaysia: Kuala Teku, Tahan Natl. Park, 1968, J. Dransfield 639 (holo SING; iso K!, L).

Root creeping, monopodially branched, flattened-subcylindrical, 0.8-1.5 mm wide (some branches thin, ca. 0.4 mm wide); ramuli on both flanks of root, usually 3-20(-30) mm long, simple or few times branched near base, with 4 or 5 branchlets; leaf deltoid, middle leaves (in 1 rank) to  $1.6 \times 1.0$  mm, lateral leaves (in 2 ranks) to  $1.7 \times 1.4$  mm, basal leaves on long ramuli patent, reduced or shorter than upper leaves. Flowering shoot associated with single or to 4 leafy sterile shoots (ramuli) 1.5-4.5 mm long, uppermost shortest; peduncle 2-4 mm long, with two bracts ca. 1 mm long at base; calyx membranaceous, 1.5-2 mm long, lobed, lobes 3, semicircular, 0.3-0.5 mm long; stamens (1-)2-3, 2-4 mm long, longer than ovary; ovary obovate-elliptic, 1.5-2 mm long, ca. 1 mm thick, 3-locular; ovules 25-35 per locule; stigmas 3, cristate, soft; capsule stalked (stalk to 3-6 mm long), obovate, 1.5-2 mm long, ca. 1 mm thick, trigonous, ribs 9.

*Distribution*: Thailand (peninsular), peninsular Malaysia.

*Notes*: *Terniopsis malayana* was believed to be endemic to peninsular Malaysia (Steenis 1972), but it occurs elsewhere in southern and northern peninsular Thailand (see also Cusset & Cusset 1988). Although *T. malayana* was described as having free central placentation (Dransfield & Whitmore 1970), an isotype and Thai materials, like those of all other species of *Terniopsis*, have axile placentation. Developmental anatomy of *T. malayana* was described by Imaichi *et al.* (1999) using material from Malaya: the ramuli and associated holdfasts

develop endogenously on the flanks of the root, and the ramulus has a shoot apical meristem.

The ramulus is variable. Plants (*TL-106*, *TL-107*) of Waeng, Narathiwat, at the southernmost end of Thailand and closest to the Malay populations, have ramuli and broad leaves as thick as in the Malay plants. In comparison, plants (*TL-411*, *TL-412*) from Phato, Chumphon, have narrower, oblong, ascending leaves, and plants (*TL-514*) from Wang Mangmai waterfalls, Khao Luang Natl. Park, Nakhon Si Thammarat, have very long (to 3 cm long), slender ramuli narrowed downward with reduced leaves.

Morphological differences do not reflect molecular similarity. Plants of *Terniopsis malayana* examined by phylogenetic analysis have almost identical *matK* sequences and identical indels, although the ramulus morphology appears very different. They also have the same *matK* sequence and indels as those of the northwestern Australian *T. australis* (Y. Kita unpubl. data; for nomenclature see the Appendix). Nonetheless, *T. malayana* is distinct from *T. australis* in the wide root (*vs.* 0.4-0.5 mm in *T. australis*), short simple shoot (but ramulus branched; *vs.* to 7 cm long, branched stem), short peduncle (*vs.* to 15 mm long), 3 stamens (*vs.* 2), and smaller ovary (*vs.* 1.5-2.3 mm long). *Terniopsis australis* appears morphologically more similar to *Tristicha trifaria* rather than to *T. malayana*, so that it has been treated as *Tr. australis* (Cusset & Cusset 1988) or *Tr. trifaria* (Aston 1990). It is likely that *T. malayana* colonized Australia and speciated into *Tr. australis* geologically recently when Australia drifted nearly to its present position close to south-eastern Asia (Kato *et al.* 2003).

*Other specimens examined*: Peninsular: Aikading stream, 35 km far from Sungai Kolok, Bala Hala Wildlife Sanctuary, Waeng, Narathiwat, 05°47.9'N, 101°49.9'E, 100 m alt., st. Mar., M. Kato *et al.* *TL-106*; Sirindhorn waterfalls, Bala Hala Wildlife Sanctuary, 35 km far from Sungai Kolok, Waeng, Narathiwat, 05°48.3'N, 101°49.6'E, 210 m alt., st. Mar., M. Kato *et al.* *TL-107*; Bang Klong Yae, Phato, Chumphon, 09°50'N, 98°47'E, 100 m alt., fl.

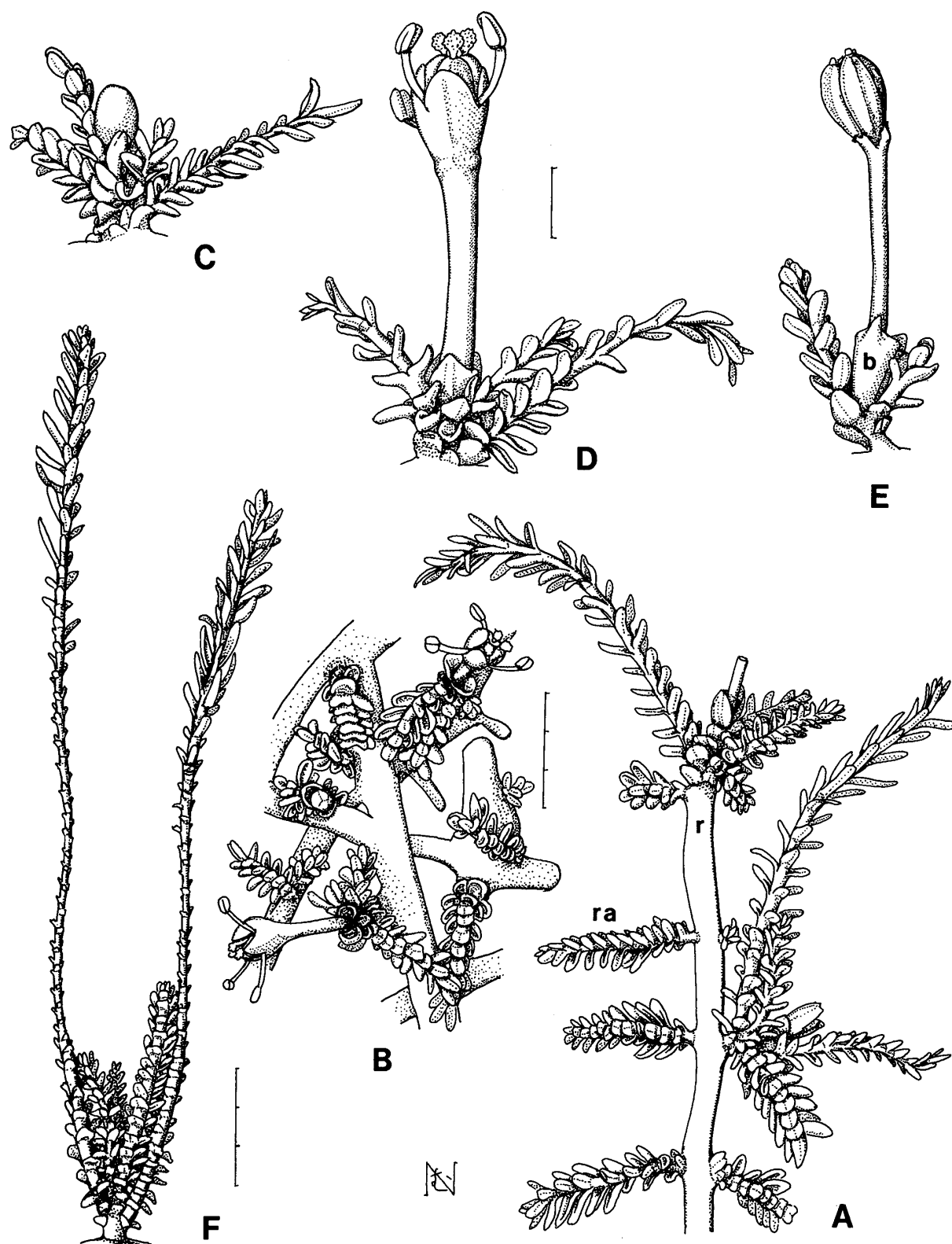


FIG. 7. *Terniopsis malayana* (A-E, M. Kato et al. TL-411; F, M. Kato et al. TL-514). A. Ribbon-like root (*r*) with ramuli (*ra*) on flanks. B. Ribbon-like roots with flowers and associate ramuli. C. Flower bud above bracts associated with short shoots. D. Flower at anthesis above bracts associated with short shoots (ramuli). E. Fruit above bracts (*b*) associated with short shoots (ramuli). F. Branched ramuli. Scales bars = 1 mm for A-E; 3 mm for F.

Dec., fr. Mar., *M. Kato et al. TL-411*, *M. Kato et al. TL-506*, *M. Kato et al. TL-507*, *M. Kato et al. TL-508*; Huay Namsainue, near Haew Lom waterfalls, Phato, Chumphon, 09°45'N, 98°40'E, 150 m alt., st. Dec., *M. Kato et al. TL-412*, *M. Kato et al. TL-510*; Kaeng Hin Dan Rapids, Nobphitam District, Khao Luang Natl. Park, 08°03'N, 99°43'E, 150 m alt., fr. Mar., *M. Kato et al. TL-518*; Ban Kraze, Lang Suan, Chumphon, *A. F. G. Kerr 11985* (BK!, K!); Wang Mangmai waterfalls, Khao Luang Natl. Park, 08°27'N, 99°47'E, 260 m alt., st. Mar., *M. Kato et al. TL-514*; Wat Kiriwong, Nakhon Si Thammarat, c. 100 m alt., st. May, *A. F. G. Kerr 15596* (BK!, K!).

**7. *Terniopsis ubonensis* M. Kato, sp. nov.** (Fig. 8)  
A congeneribus radicibus latissimo (usque ad 10 mm), pedunculis (usque ad 12 mm) et staminibus longissimo (usque ad 6 mm), ovulis in loculus 8-12 differt.

*Typus*: Kaeng Saphue, Moon River, Ubon Ratchathani, Eastern Thailand, 15°15'N, 105°15'E, Feb. 19, 110 m alt., 2005 (fl.-buds, fl. [fr.]), *M. Kato, S. Koi & T. Wongprasert TL-1308* (holo BKF; iso TI, TNS).

Root creeping, monopodially branched, broadly ribbon-like, variable in width, (1-)2-10 mm wide; ramuli on both flanks of root, usually 10-90 mm long, simple or a few times branched near base with to 4 or 5 ramulus branchlets; leaves tristichous, ascending, with single vein, leaves on long shoot separated, oblong, 1.5-2 mm long, 0.6-1 (-1.3) mm wide, leaves on short shoot imbricate, elliptic or oblong-elliptic, 1-1.5 mm long, 1-1.2 mm wide. Flowering shoot associated with single or to 4 leafy sterile shoots (ramuli), 1.5-3 mm long; peduncle 7-15 mm long, with 2 bracts ca. 1 mm long at base, bracts broader than leaves; calyx membranaceous, 1.5-1.7 mm long, shorter than ovary at anthesis, shallowly lobed, lobes 3, semicircular, 0.3-0.5 mm long, later often more deeply incised; stamens (1-)2-3, caducous (protandrous?), 5-6 mm long including anthers, much longer than ovary; anthers ca. 1 mm long, sagittate; ovary obovoid-ellipsoid, 1.5-2 mm long, ca. 1 mm thick, 3-locular;

ovules 8-12 per locule, borne on upper and lower parts of septum, separated by sterile middle part; stigmas 3, separate, cristate, 0.5-0.7 mm long and wide; capsule stalked (stalk 5-15 mm long), obovate, 1.5-2 mm long, ca. 1 mm thick, trigonous, ribs 9.

*Distribution*: Thailand (southeastern).

*Notes*: *Terniopsis ubonensis* differs from all congeneric species in the root being markedly variable in width (2-10 mm), the peduncle long (7-12 mm), the stamens 3 times longer than the ovary, and the ovules per locule fewer (8-12). The root is the widest of the Asian species of Podostemaceae with ribbon-like roots except for *Polypleurum stylosum* (Wight) J.B.Hall with roots to 23 mm wide (Mathew & Satheesh 1997). It may be due to either extensive marginal growth proximal to the apical growth or secondary widening, because the young root is only as wide as the ribbon-like root. The peduncle is as long as that of *Terniopsis ramosa* (6-9 mm), from which the present species differs in having two bracts. Further comparison is needed with *T. ramosa*, because of poor collections of the latter. The stamens are the longest (5-6 mm) in the genus, although stamen length is not well known for *T. ramosa*. The most remarkable character is the number of ovules. *T. ubonensis* is distinctive in the genus and even from other genera of Tristichioideae in that the ovules are borne on the upper and lower parts of the septa separated by the middle thick septa, as in species of Podostemoideae.

Surprisingly, *Terniopsis ubonensis* is a member of the "*Terniopsis*" clade. It is morphologically very similar to *T. australis* and *T. malayana* of the "*Malaccotristicha*" clade, except in the placentation, while *T. sessilis* of the "*Terniopsis*" clade is similar to *T. brevis* and small plants of *T. malayana* rather than to *T. ubonensis*.

*Other specimens examined*: *M. Kato et al. TL-1306*, *TL-1307*, *TL-1309* from the same locality as the type.

**8. *Terniopsis brevis* M. Kato, sp. nov.** (Fig. 9)  
A *T. malayana* plantis parvis, ramulis usque bre-

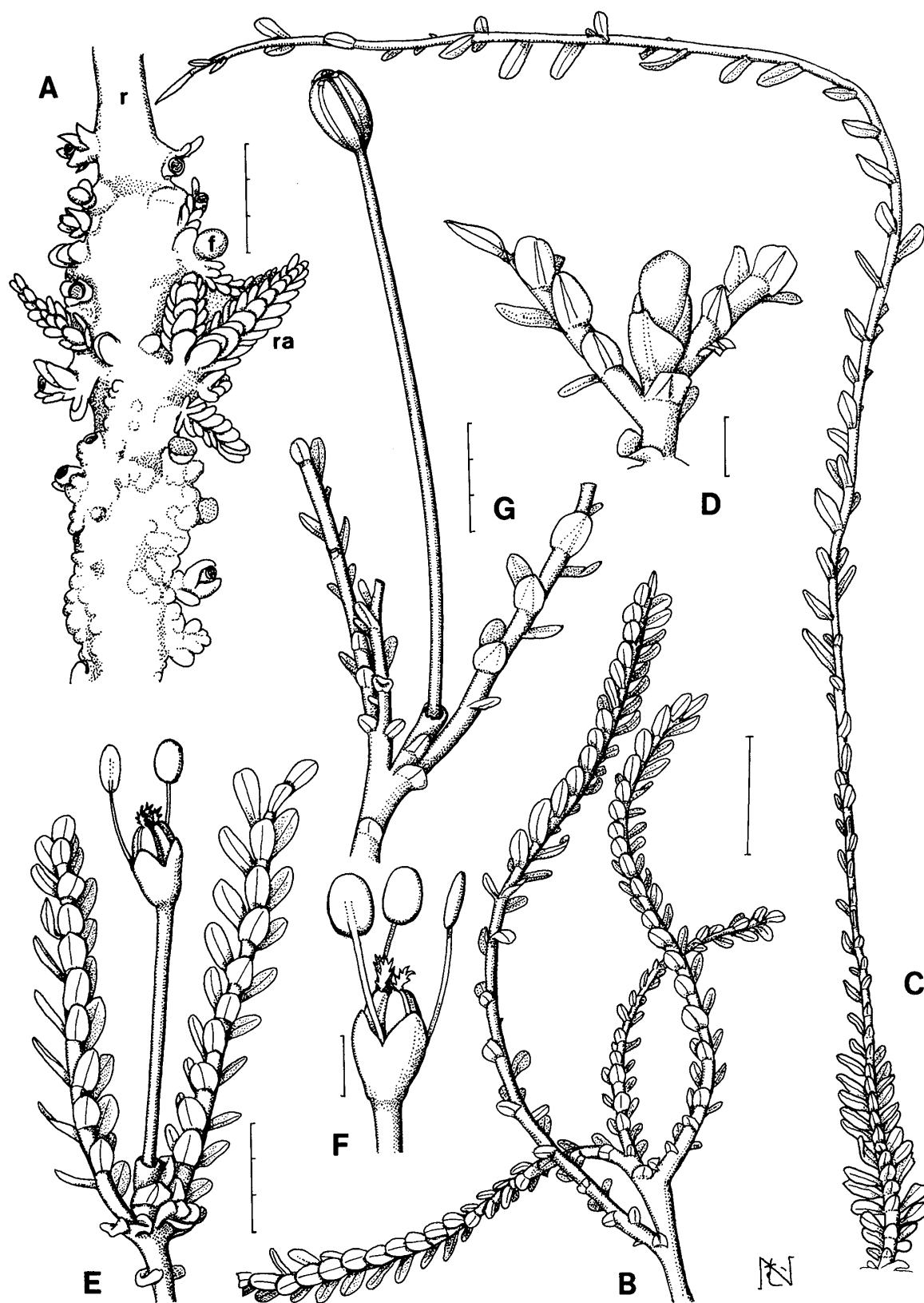


FIG. 8. *Terniopsis ubonensis* (B-G, M. Kato et al. TL-1308, type; Kato et al. TL-1307). A. Ribbon-like root (r) with ramuli (ra) and flower buds (f) on flanks. B. Branched ramuli. C. Ramulus. D. Flower bud above bracts associated with short shoots (ramuli). E. Flower at anthesis above bracts associated with short shoots (ramuli). F. Flower. G. Fruit above bracts associated with short shoots. Scales bars = 3 mm for A, E, G; 1 mm for B-D, F.

vibus, ad 3.5 mm longis, foliis semiellipticis, usque ad 0.9 mm longis, staminibus 2 differt.

*Typus*: Kaeng Lamduan stream, Yoddome Wildlife Sanctuary, Ubon Ratchathani, eastern Thailand, 14°26'N, 105°6'E, 150 m alt., Dec. 29, 2000 (fl. fr.), M. Kato, Y. Kita & T. Wongprasert TL-321 (holo BKF; iso TI, TNS).

Root creeping, monopodially branched, flattened-subcylindrical, 0.2–1 mm wide; ramuli on both flanks of root, 2.2–3.5 mm long, simple; leaves in 3 ranks, oblong-elliptic, middle leaf to 0.8 mm × 0.4 mm, lateral leaf to 0.9 mm × 0.5 mm. Flowering shoot associated with single sterile ramulus, sterile ramulus 1–2 mm long; peduncle with 2 bracts at base, to 3 mm long; calyx membranaceous, shallowly 3-lobed or lobed 1/4 to base, as long as ovary; stamens 2, rarely 3, as long as ovary, 1–1.2 mm long; ovary obovoid-ellipsoid, 1–1.3 mm long, ca. 0.8 mm thick, 3-locular; stigmas 3, separated from each other, oblong, apex cristate or subcristate, 0.3 mm long; ovules 13–20 per locule; capsule stalked (stalk to 3.5 mm long), trigonous, ribs 9.

*Distribution*: Thailand (central, eastern, peninsular).

*Notes*: *Terniopsis brevis* differs from *Terniopsis malayana* in its smaller size, e.g., short ramuli, smaller leaves, smaller flowers and fruits with 2 (vs. 3) stamens and fewer ovules (13–20 vs. 25–35). However, in a young plant of *T. malayana* the shoot is to 7 mm long with leaves deltoid to semielliptic, the dorsal ones to 0.8 mm × 0.6 mm, the lateral ones 1.0 mm × 0.4 mm. Similarity of the mature plant of *T. brevis* to the young plant of *T. malayana*, along with the smaller flowers, suggests paedomorphic derivation.

Plants (TL-60, TL-309) from Khao Yai Natl. Park, central Thailand, are tentatively referred here. Although they are nearly impossible to separate from the eastern and peninsular populations, there are unique indels in the *matK* sequences and different *matK* sequences by which the Khao Yai pop-

ulations can be segregated (Y. Kita unpubl. data). In the Khao Yai population only vegetative plants have been collected. In December, January and February of three different years during the dry season the plants were always submerged on rock surfaces 30–60 cm under the water surface, while sympatric populations of *Hydrobryum khaoyaiense*, *Cladopus taiensis*, and *Polypleurum wallichii* var. *parvum* were exposed and produced flowers or fruits. It is likely that the Khao Yai population reproduces vegetatively by plant parts or regenerative buds that are dispersed by fish (unpubl. observation), or rarely produces flowers when the water drops more in extremely dry seasons. It is also possible that other unknown populations reproduce sexually.

The seedling development of *Terniopsis brevis* was described by Kita & Kato (2005), who treated it as an undescribed species of *Malaccotristicha*. The young seedling has a small primary shoot apical meristem and a primary root apical meristem. The shoot meristem develops into a plumular ramulus, and the root meristem into a cylindrical radicle with no root cap and then into a flattened, capped primary root. An adventitious root develops on the lateral side of the hypocotyl. This pattern is similar to that of most angiosperms, but differs from the described patterns of Podostemaceae.

*Other specimens examined*: Eastern: Kaeng Lamduan stream, Yoddome Wildlife Sanctuary, Ubon Ratchathani, 14°26'N, 105°6'E, 150 m alt., fl. fr. Dec., M. Kato et al. TL-320B. Central: Haew Narok waterfalls, Khao Yai Natl. Park, Nakawn Nayok, 14°17'N, 101°24'E, 360 m alt., st. Dec., Jan., Feb., M. Kato et al. TL-60, M. Kato et al. TL-309, M. Kato & T. Wongprasert TL-1105. Peninsular: Klong Kamphuan stream, Kong Nakha Wildlife Sanctuary, Sooksamran, Ranong, 09°21'N, 98°27'E, 150 m alt., st. Dec., M. Kato et al. TL-414, M. Kato et al. TL-511, A. F. G. Kerr 16872 (BK!).

**9. *Terniopsis ramosa* M. Kato, sp. nov.** (Fig. 10) *Terniola diversifolia* Lecomte, Not. Syst. 1: 7, 1909; Fl. Gén. Indochin. 5: 43, 1926, p.p. excl. basionym – *Dalzellia diversifolia* (Lecomte) C. Cusset, Fl. Cambodge, Laos, Viêt-Nam 14: 78, 1973, p.p. excl.



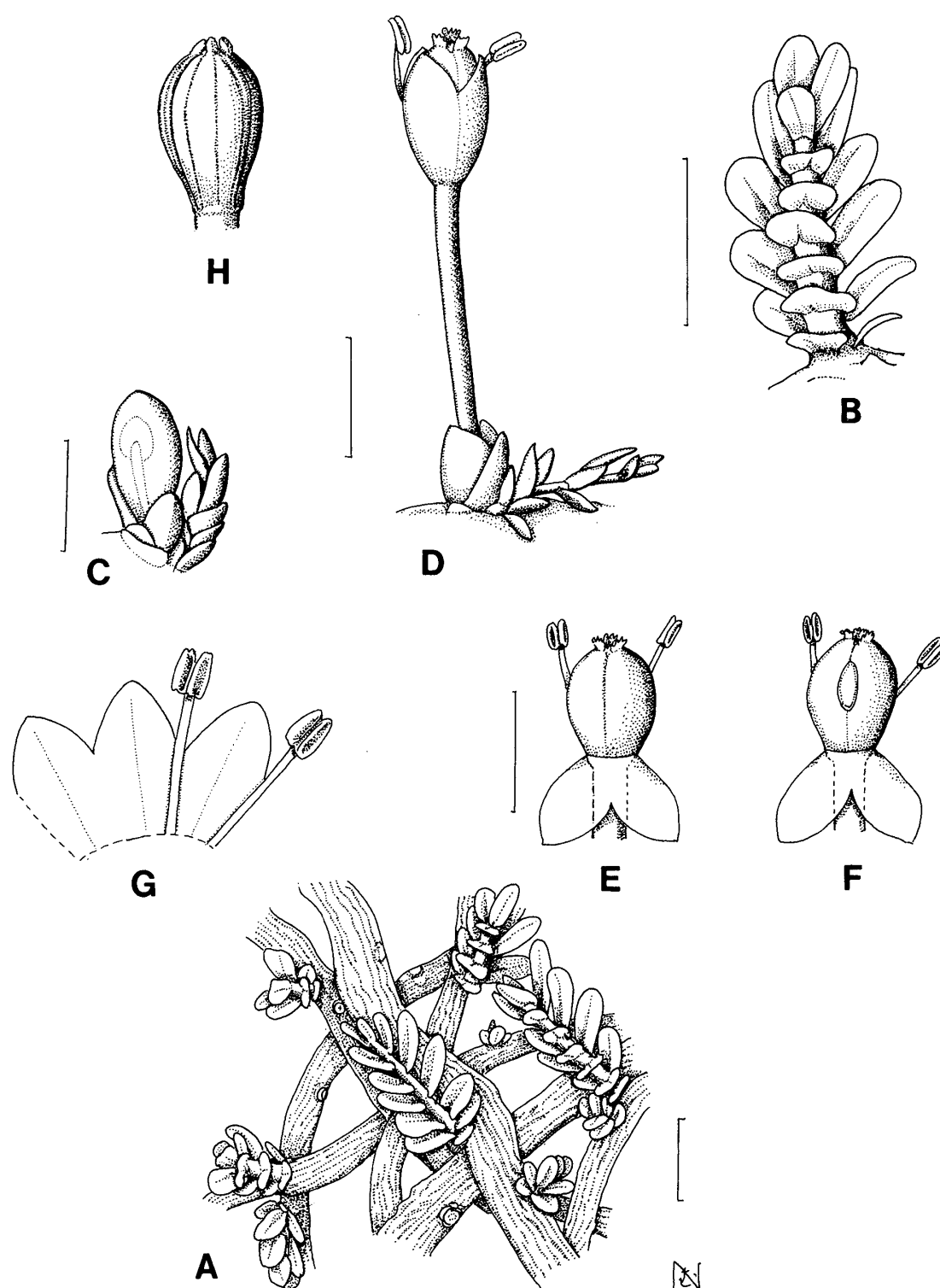


FIG. 9. *Terniopsis brevis* (Kato et al. TL-321, type). A. Ribbon-like roots with ramuli on flanks. B. Ramulus with tristichous leaves. C. Flower bud above bracts associated with short shoot (ramulus). D. Flower at anthesis terminating peduncle. E, F. Flowers with tepals artificially reflexed. G. Trilobed tepal and two stamens. Note that stamen is absent on side facing the associated ramulus in D, E, G. H. Fruit. Scale bars = 1 mm.

basionym; Cusset & Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 10(2): 173, 1988, p.p. excl. basionym.

A *T. malayana*, *T. brevis* et *T. tenui* caulibus saepe ramosis, basaliter 1.5 mm crassis, sparsim foliosis differt; *T. australis* caulibus ramosis similis sed foliis sparsis, coriaceusis, staminibus 3 differt. *Indotristicha ramosissima* caulibus ramosis similis sed caulibus brevibus, foliis ramulorum 3-fariis differt.

*Typus*: Ubon, eastern Thailand, anno 1866-1868, *C. Thorel 2791bis* (P!). Specimen *C. Thorel 2791* includes two species, *Cussetia diversifolia* (= *Terniola diversifolia*) and *Terniopsis ramosa*, on the same sheet. For the species name *Terniola diversifolia* and typification, see Notes under the species above. The holotype of *Terniopsis ramosa* is numbered here as *C. Thorel 2791bis* and should be separated from *C. Thorel 2791*.

Root ribbon-like, ca. 2 mm wide, with shoots on dorsal surface. Shoot few times branched at proximal part (branching usually anisotomous, dichotomous or nearly trichotomous), frequently branched at distal part, swollen (holdfast?) at base, to 3 cm long or longer, ca. 1.5 mm thick, sparsely leafy, leaves deltoid-semicircular, ca. 1.5 mm × 1.5 mm, thick, irregularly arranged. Flowering shoots usually associated with single vegetative shoots (ramuli), associating shoot 3-5 mm long, leaves in 3 ranks, imbricate, ovate, apex obtuse, coriaceous, with thick, broad midrib, ventral-lateral leaves ca. 1 mm × 0.7 mm, dorsal ones ca. 1 mm × 1 mm, both gradually smaller upwards; bracts several, the uppermost covering flower bud, similar to dorsal leaves, larger (ca. 1.5-2 mm long), phyllotaxis spiral or irregular (not 3-ranked); peduncle 6-9 mm long, calyx membranaceous, lobed ca. 1/4 to base, lobes 3, ca. 2 mm long, with midrib; stamens 3; ovary 3-locular, obovoid-ellipsoid, apex subtruncate, ca. 2 mm × 1.2 mm, placentation axile; stigmas 3, separate from each other; capsule stalked,

trigonus, ribs 9.

*Distribution*: Thailand (eastern).

*Notes*: For nomenclature, see Notes for *Cussetia diversifolia* above. *Terniopsis ramosa* has been confused with *Cussetia diversifolia*, which was probably collected together at the same site. Diagnostic characters to distinguish *Terniopsis* from *Cussetia* are given in the key and in the Notes for *Terniopsis* above.

*Terniopsis ramosa* differs from *T. malayana* and *T. brevis* in Thailand and Malaysia in the long, branched shoots. It is similar to the Australian *T. australis* in the branched shoots but differs in the sparse, coriaceous leaves on the proximal portion of the stem and the three stamens. Several bracts differentiate it from related species with two bracts. *Terniopsis ramosa* is also similar to *Indotristicha ramosissima* from southern India in the branched, leafy shoot with irregular phyllotaxis, and may be referable to the genus *Indotristicha*, pending further examination. It differs in the shoots being much shorter (to 3 cm long), branched fewer times (at most several times), lacking in leaf dimorphism (linear and broad), and trifariate phyllotaxis on the ramuli. Analysis and recollection is needed to understand the phylogenetic relationship and morphology of the species.

#### Subfamily Podostemoideae Engl.

in Engler & Prantl, Nat. Pflanzenfam. 18a: 36, 1830; Royen, Meded. Bot. Mus. Herb. Univ. Utrecht 107: 13, 20, 1951; Melchior, Engler's Syllab. Pflanzenfam. 12th ed. 2: 245, 1964; Takhtajan, Div. Classif. Fl. Pl. 269, 1997; Rutishauser, Aquat. Bot. 47: 62, 1997 - Podostemaceae Richards ex C. Agardh; Willis, J. Linn. Soc., Bot. 43: 51, 1914; Cusset, Fl. Cambodgia, Laos, Viêt-Nam 14: 65, 1973; Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 14(1): 13, 1992. *Typus*: *Podostemum* Michx.

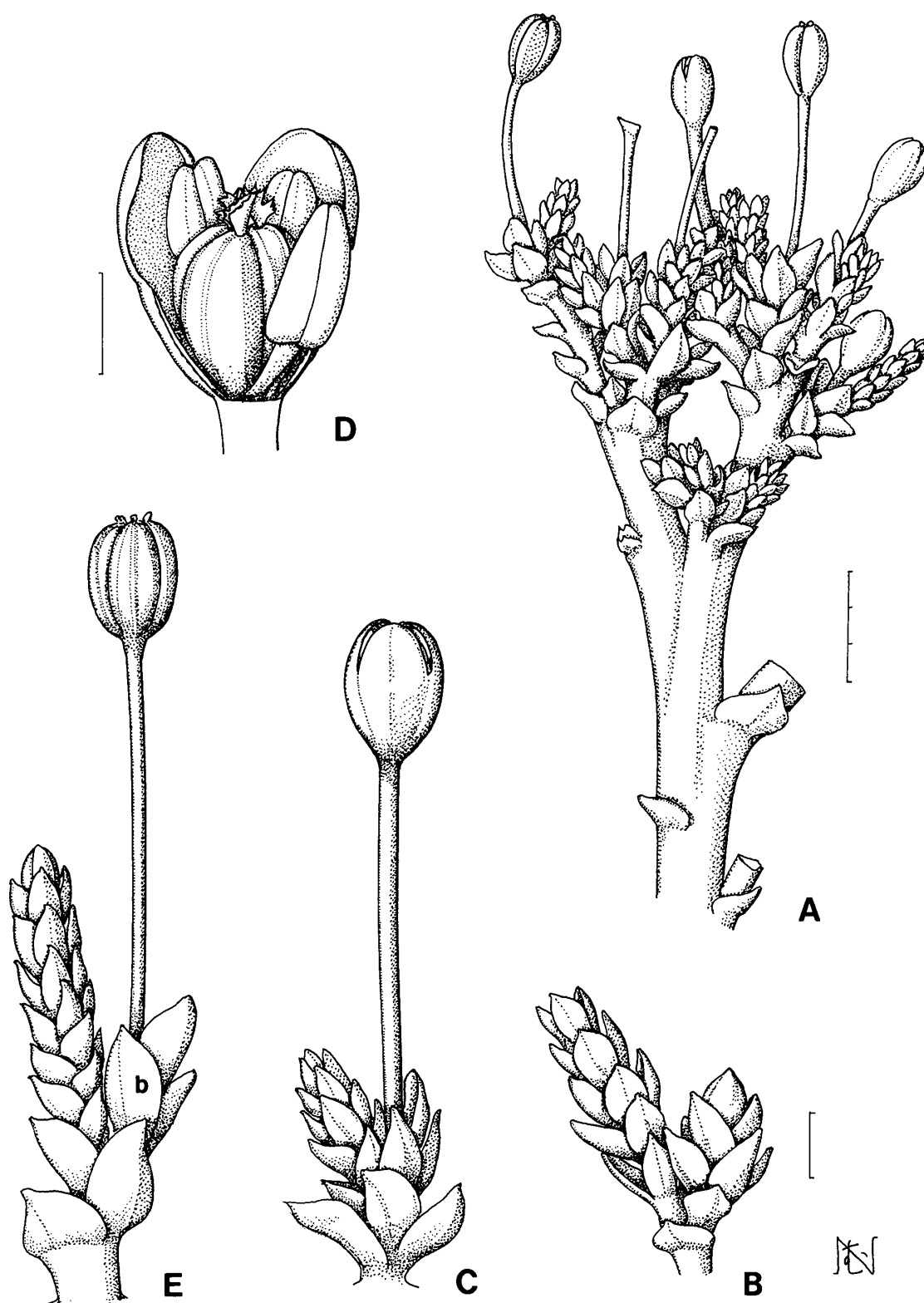


FIG. 10. *Terniopsis ramosa* (C. Thorel 2791bis [P], type; herbarium specimen). A. Reconstruction of branched, flowering and fruiting shoot. Flowers and fruits except one fruit is drawn artificially connected to the peduncle. B. Flower bud above bracts (right) associated with short shoot (ramulus; left). C. Flower at anthesis on peduncle associated with short shoot (ramulus). D. Flower bud opened to show internal structure. Stamens are alternate tepals. E. Fruit above bracts (*b*) and short shoot (ramulus). Scale bars = 3 mm for A; 1 mm for B-E.

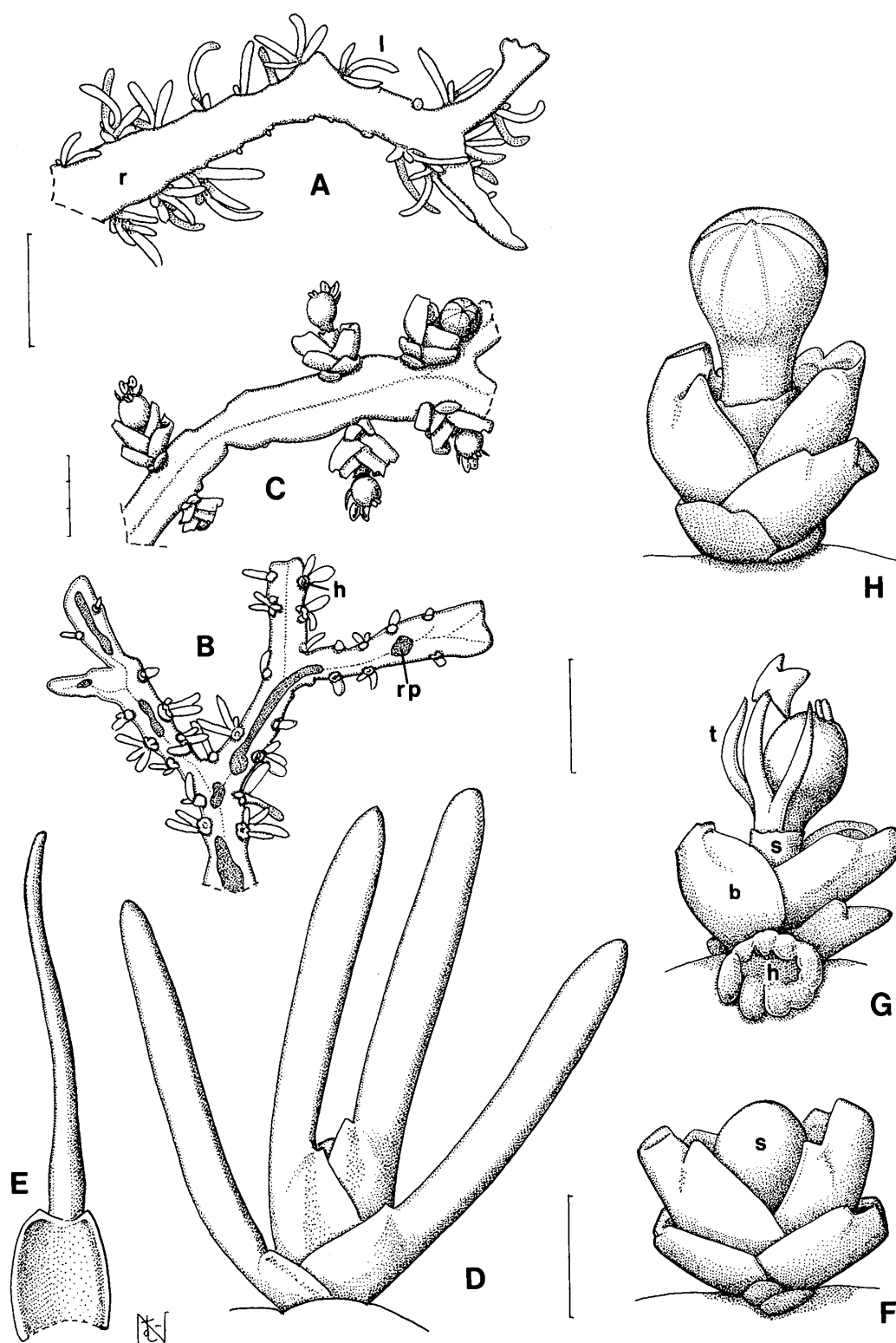


FIG. 11. *Paracladopus chiangmaiensis* (Kato et al. TL-808, type; E, F, M. Kato et al. TL-1005). A, B. Dorsal (A) and ventral (B) views of ribbon-like roots (*r*) with tufts of leaves (*l*) on flanks. Note rhizoid pads (*rp*) along roots and holdfasts (*h*) at base of leaf tufts (B). C. Root with flowering shoots. D. Lateral view of ensiform bracts covering flower bud. E. Adaxial view of bract trilobed at base and distally ensiform. F. Flower bud covered by spathe (*s*) above bract bases. Ensiform portions have fallen. G. Ventral view showing holdfast (*h*) and flower with tepals (*t*) above ruptured spathe and bracts (*b*). H. Young fruit; dorsal view. Scales bars = 5 mm for A, B; 3 mm for C; 1 mm for C-H.

Root adhering to rock surface by rhizoids or also holdfasts on ventral surface, ribbon-like or crustaceous (species with such roots treated in Kato 2004), with tufts of leaves or long shoots at root branch points, on/near both flanks along the length, or scattered on surface; leaves needle-like, linear, linear-lanceolate, or linear-oblong, obtuse or pointed. Bracts 2-many in 2 or 4 ranks (*Hanseniella*), uniform or dimorphic. Flower 1 on shoot apex, zygomorphic, bud covered by globose or ellipsoid glabrous spathe; tepals 2, one on each side of stamen, linear; ovary 2- or rarely 1-locular; stamens 1 or 2 (forked); ovules on septum surface or along marginal surface (in unilocular ovary); stigmas 2; capsule smooth or ribbed. Genera ca. 40, 6 in Thailand (*Cladopus*, *Paracladopus*, *Polypleurum* treated here; crustaceous-rooted *Hanseniella*, *Hydrobryum*, and *Thawatchaia* [Kato 2004]).

*Notes:* Asian Podostemoideae are usually small due to reduction of the shoot, compared with some American genera with large shoots or leaves (e.g., *Apinagia*, *Marathrum*, *Mourera*, *Rhyncholacis*, *Vanroyenella*). Exceptionally, the Asian *Polypleurum longicaule* and *P. erectum*, and perhaps *Diplobryum koyamae* M.Kato & Fukuoka and *D. ramosum* C.Cusset have long shoots (Kato & Fukuoka 2002). The root is either ribbon-like with tufts of leaves on/near both flanks along the root in *Cladopus*, *Paracladopus* and *Polypleurum* treated here, or crustaceous with tufts of leaves scattered on the dorsal surface in *Hanseniella*, *Hydrobryum* and *Thawatchaia* (Kato 2004). The difference in root morphology between the two is great, but the root of some species, e.g., *C. javanicus* M.Kato & Hambali and *Zeylanidium maheshwarii* C. J. Mathew & Satheesh, is broadly ribbon-like and elongate-crustaceous, respectively, showing somewhat intermediacy. The flower is 2-merous in the number of ovary locules and stigmas; the stamen is simple or forked with a common andropod (vs. multiple in some American genera). Phylogenetic studies show that Asian Podostemoideae form a monophyletic

clade (Kita & Kato 2001) indicating that their morphologies have diversified a common ancestor.

### ***Paracladopus* M. Kato, gen. nov.**

#### **10. *Paracladopus chiangmaiensis* M. Kato, gen. et sp. nov.** (Fig. 11)

*Cladopus radibus taeniatis*, staminibus 1, capsulis globosis, laevigatis similis, sed haptero in latere ventrali radicis infra caespites foliorum, caespitibus foliorum multis secus longitudinem radicis, foliis ensiformibus, basi vaginatis, bracteis anguste triangularibus basi lobatis, superne ensiformibus differt.

*Typus:* Mae Wang stream, north of Doi Inthanon Nalt. Park, Chiang Mai, Northern Thailand, 18°38'N, 98°43'E, 450 m alt., Mar. 31, 2003 (fl. fl.-buds & fr.), M. Kato, R. Imaichi & T. Wongprasert TL-808 (holo BKF, iso TI, TNS).

Root creeping, adhering to rock surface by rhizoid pads distributed in middle of root and by holdfasts at shoot bases on ventral surface, isotomously and anisotomously branched, ribbon-like, 1.5-2 mm wide, with tufts of leaves at edge on both flanks, roughly 2-3 mm apart, in no relation to root branching and at every point of root branching; holdfasts one or few per shoot base, short or cylindrical, 0.5-1 mm long, 0.2-0.3 mm thick; leaves to 5 per tuft, sheathed at base, ensiform with lamina flat in adaxial-abaxial plane, linear-oblong or linear-oblongate, sometimes with 2 small lobes at base, apex obtuse, 2-3.5 mm long. Flowering shoot very short; bracts 4 or 5 in two ranks, when young (subtending flower buds) usually linear-oblong, ensiform, 3-4 mm long, sheath-like with 2 small lobes at base, caducous, broken above base at bud maturity, remaining base trilobed, 1-3 mm long, ca. 1 mm wide; flower 1, peduncle to 0.5 mm long, bud covered by spathe, spathe ellipsoid, smooth, irregularly rupturing near apex at anthesis; tepals 2, 1 on each side of stamen, linear, ca. 0.8 mm long; stamen

1, 1-1.2 mm, anthers caducous, filaments as long as ovary; ovary globose, ca. 1 mm long and thick, 2-locular, with 2 vertical grooves; stigmas 2, forked, 0.1-0.2 mm long, linear to narrowly deltoid, entire, withered at anthesis; ovules borne on entire septum surface, 20-27 per locule. Capsule shortly stalked (stalk ca. 0.5 mm long), globose, slightly compressed, ca. 1 mm long and wide, smooth but with weak narrow stripes, dehiscing by 2 equal valves.

*Distribution.* Thailand (northern).

*Notes.* This new genus, *Paracladopus*, is most similar to *Cladopus* in the single stamen and globose, smooth ovary. It is distinct from *Cladopus*, however, in having holdfasts at the base of all tufts of leaves (shoots) on the ventral surface of the root, many tufts of leaves borne along the length of the root on both flanks without relation to root branching and at all root branches, ensiform leaves with sheaths on the inner edge, bracts narrowly deltoid with two small lateral lobes and one ensiform, caducous middle lobe, and weak narrow stripes on the capsule. The stripes on the capsule are as inconspicuous as those of *C. queenslandicus* (Domin) C. D. K. Cook & Rutish., while they are smooth in other species of *Cladopus*. Although *Paracladopus chiangmaiensis* and *C. queenslandicus* also share trilobed bracts, the bracts (*i.e.*, leaves on the floriferous shoot) are much fewer, shorter in the former and with the middle lobe dorsiventral in the latter. In *Cladopus* there is no holdfast for adhesion to rock surfaces, the tufts of leaves are borne exclusively at every root branching point and are absent between branch points, and the bracts are usually digitate and, like the leaves, are dorsiventral. Molecular phylogenetic analysis (Y. Kita unpubl. data) shows that *Paracladopus* is sister to *Cladopus*, and the two genera are in turn sister to the clade of the crustaceous-rooted *Hanseniella*, *Hydrobryum* and *Thawatchaia*.

Although the ensiform leaves and bracts of *Paracladopus chiangmaiensis* are unique in the *Cladopus-Hydrobryum* group, they are not rare in

Podostemoideae. There are such leaves in, *e.g.*, American *Apinagia*, *Marathrum*, *Mourera*, *Ozerya*, *Podostemum*, and *Rhyncholacis* (Rutishauser 1995, 1997, Rutishauser & Grubert 2000, Jäger-Zürn 2002, 2003, R. Imaichi unpubl. data), Asian *Zeylanidium* (as *Podostemum*, Jäger-Zürn 2000), and the African *Endocaulos* and *Thelethylax* (R. Imaichi unpubl. data). The leaves are flattened in an adaxial-abaxial orientation with the basal sheath on the inner (adaxial) edge. Hence, the root leaf (or tuft of leaves) system is dorsiventral with the upper surface toward the light and the lower surface toward the rock. There is a controversy in the evolutionary interpretation of the ensiform leaf. Rutishauser (1997) explains it as a 90° switch in the dorsiventrality of the leaf primordium, while Jäger-Zürn (2002) interpreted it as a modification due to intercalary growth in the dorsal surface of the leaf. Close observations are necessary to understand the ensiform leaf of *P. chiangmaiensis*.

*Other specimen examined:* Northern: Mae Wang stream, east of Doi Inthanon Natl. Park, Chiang Mai, 18°38'N, 98°43'E, 450 m alt., fl.-buds Dec., *M. Kato et al. TL-1005*.

### **Cladopus** H. Möller

Ann. Jard. Bot. Buitenzorg, ser. 2, 1: 115, 1899; Engler, Nat. Pflanzenfam. 2nd ed. 18a: 50, 1930; Steenis, Fl. Males. I, 4: 65, 1949; Backer & Bakhuizen van den Brink, Fl. Java. 1: 204, 1963; Ohwi, Fl. Japan 394, 1965; Cusset, Fl. Cambodge, Laos, Viêt-Nam 14: 71, 1973; Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 14(1): 20, f. 1, 2, 1992; Kato & Kita, Acta Phytotax. Geobot. 54: 90, 2003; Qiu & Philbrick, Fl. China 5: 191, 2003. *Typus:* *Cladopus nymanii* H. Möller.

*Lawiella* Koidz., in Doi, Fl. Satsum. 1(2): 21, 1927; emend. Koidzumi, in Doi, Fl. Satsum. 2: 94, 1931; Acta Phytotax. Geobot. 4: 23, 1935; Chao, Contr. Inst. Bot. Natl. Acad. Peiping 6(1): 5, 1948. *Typus:* *Lawiella doiana* Koidz.

*Hemidistichophyllum* Koidz., in Doi, Fl. Satsum. 1(3): 24, 1928. *Typus:* *Hemidistichophyllum*

*japonicum* (Imamura) Koidz.

*Lecomtea* Koidz., in Doi, Fl. Satsum. 1(4): 52, 1929. *Typus*: *Lecomtea pierrei* (Lecomte) Koidz.

Root creeping, adhering to rock surface by rhizoids, ribbon-like, branched, with lateral branches on both flanks, with tufts of leaves near edge on both flanks at all branch points; leaves linear, flat, apex obtuse. Flowering shoot very short, with bracts in two ranks, lobed or digitate; flower 1, at shoot apex, bud covered by spathe, spathe globose, irregularly ruptured near apex at anthesis; tepals 2, 1 on each side of stamen at uppermost part of short peduncle; stamen 1, as long as ovary; ovary globose-ellipsoid, with 2 grooved vertical lines, 2-locular; stigmas 2, forked near base, linear to subulate, entire; ovules covering entire septum surface. Capsule stalked, globose, smooth (not obviously ribbed), dehiscent by 2 valves. Species ca. 10, 2 in Thailand.

*Distribution*: Thailand, southern Laos, southern Vietnam, south-central and southeastern China (Hainan, Guangzhou, Fujian), southern Japan (Kyushu), Indonesia (western East Kalimantan, Java, southern Sulawesi, Flores), southeastern Papua New Guinea, northeastern Australia (northern Queensland).

*Notes*: *Cladopus* is distinguished from other genera (except *Paracladopus*) in its globose, smooth capsule and digitate or multilobed bract. Cusset (1973, 1992) delimited the genus in a broad sense by the globose, smooth capsule. In Cusset's classification, *Cladopus* comprises two sections, *Cladopus* and *Griffithella*, distinguished by the number of stamens (1 vs. 2). In comparison, Mathew & Satheesh (1997) treated the two as independent genera. *Cladopus hookerianus* (Tul.) C.Cusset and *C. pierrei* (Lecomte) C.Cusset of sect. *Griffithella* differ in the root being disk-like (20-50 mm wide and bearing flowers at margin) in *C. hookerianus* vs. ribbon-like (to 5 mm wide) in *C. pierrei*, and the bracts being simple, narrowly deltoid, pointed, and

hooded in *C. hookerianus* vs. digitate in *C. pierrei*. *Cladopus pierrei* is similar to species of sect. *Cladopus* in the bract being digitate, rough-surfaced and the flowering shoots borne on the root at the point of branching. Similar variation in the number of stamens also exists in *Polypleurum* and *Hydrobryum*. Hence, *Lecomtea*, typified by *C. pierrei*, is treated as synonymous with *Cladopus*, but *Griffithella*, typified by *C. hookerianus*, may better be segregated from *Cladopus*, as classified by Warming (1901) and Mathew & Satheesh (1997). Treated as such, *Cladopus* does not occur in southern India. Further phylogenetic analysis is needed to clarify the relationships of *Cladopus* and *Griffithella*.

The species taxonomy remains unsettled. Cusset (1992) recognized four species in *Cladopus*. In his treatment section *Cladopus* contains two species, i.e., the variable and widely distributed *C. nymanii* sensu lato and *C. taiensis* endemic to Thailand, and sect. *Griffithella* consists of *C. pierrei* of Laos and Vietnam and *C. hookerianus* of southern India. In contrast to Cusset's (1992) lumping of *C. nymanii* H.Möller, some authors (e.g., Chao 1948, Kadono 1994, Kadono & Usui 1995) recognized four local species in Japan (*C. austro-osumensis* Kadono & N.Usui, *C. austrosatsumensis* (Koidz.) Ohwi, *C. doianus* (Koidz.) Koriba, *C. japonicus* Imamura) and two species in China (*C. chinensis* H.-C.Chao, *C. fukiensis* H.-C.Chao). Recently Kato & Hambali (2001) described *C. javanicus* from West Java, and Kato & Kita (2003) reduced *C. austrosatsumensis* and *C. chinensis* to *C. japonicus* and described a new species, *C. austrosinensis* M. Kato & Y. Kita. *Cladopus queenslandicus* of northeastern Australia and Papua New Guinea has long been treated as the sole species of the genus *Torrenticola* (Steenis 1949, Aston 1990, Cusset 1992, Cook 1996), but was recently transferred to *Cladopus* (Cook & Rutishauser 2001). As a result, *Cladopus* comprises about 10 species. In a molecular phylogenetic analysis, *Cladopus* is divided into two clades, one of which is a Southeast

Asian clade of *C. nymanii* sensu stricto, *C. queenslandicus* and *C. javanicus* along with *C. fallax* and *C. taiensis*, while the other is an East Asian clade of the Chinese and Japanese species (Kita & Kato 2001, 2004a).

Cusset (1992) recognized *C. taiensis* from Thailand, and here I add *C. fallax*. Although Royen (1965) reported *C. nymanii* sensu lato from Thailand (see Notes of *C. taiensis* and *C. fallax* below), most likely *C. nymanii* sensu stricto does not occur there (Kato & Hambali 2001, Kita & Kato 2004b).

**11. *Cladopus taiensis*** C. Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 14(1): 24, f. 2. 1-3, 1992 (Fig. 12). *Typus*: Fang, Chiang Mai, northern Thailand, Feb. 21, 1959 (fl.), *T. Smitinand* 4447 (C!).

Root creeping, adhering to rock surface, ribbon-like, 2-2.5 mm wide, monopodially or anisotomously branched, with tufts of leaves near edge on both flanks of root at all branch points; leaves to 5 per tuft, linear, flat, apex obtuse, to 2.5 mm long. Flowering shoot short; bracts 4(-6), in two ranks, lobed, 0.5-0.8 mm long, 0.8-1 mm wide; lobes 3 or 4, thin, semicircular, smooth; flower 1, peduncle 1-1.5 mm long, bud covered by spathe, spathe globose, submucronate, irregularly ruptured near apex at anthesis; tepals 2, 1 on each side of stamen, linear, to 0.6 mm long; stamen 1, to 1.7 mm long, as long as ovary; ovary globose-ellipsoid, 1-1.2 mm long, 0.7-1 mm thick, 2-locular, with 2 vertical grooves; stigmas 2, forked near base, 0.3-0.5 mm long, linear to subulate, entire; ovules on septum surface, 18-23 per locule. Capsule stalked (stalk to 2 mm long), globose, smooth.

*Distribution*. Thailand (northern, northeastern, central)

*Notes*. *Cladopus taiensis* is different from *C. fallax* and all other congeneric species in the semicircular, thin bract lobes. In a molecular phylogenetic tree, *C. taiensis* is sister to, and obviously

separated from *C. fallax* and together they are basal in the Southeast Asian clade (see Notes under *Cladopus*) (Kita & Kato 2004a). *Cladopus taiensis* is the northernmost species of the Southeast Asian clade, which occurs in southeastern Thailand and southern Vietnam (*C. fallax*), Indonesia (Java, Kalimantan?, southern Sulawesi, Flores) (*C. nymanii*), Java (*C. javanicus*), eastern Papua New Guinea and northeastern Australia (*C. queenslandicus*).

*K. Larsen* 31813 with only mature fruits is tentatively identified as *C. taiensis*, pending further collections in northeastern Thailand.

*Other specimens examined*: Central: Wang Takrai Falls, Nakhon Nayok, 14°20'N, 101°18'E, 65 m alt., fl. Dec., Mar., *M. Kato et al.* TL-101, TL-102, TL-302; Nang Rong waterfalls, Khao Yai Natl. Park, 14°20'N, 101°19'E, 50 m alt., st. Sep., fl. Dec., Mar., *M. Kato et al.* TL-103, TL-202, TL-304, *M. Kato & T. Wongprasert* TL-603, TL-604, *T. Smitinand* s.n. (C); Haew Narok Falls, Khao Yai Natl. Park, ca. 500 m alt., fl. Dec., *T. Wongprasert et al.* s.n. (BKF), E. Sarika, Nakhon Nayok, fl. Feb., *Jacobsen* 77-31 (C), Northeastern: 15 km NE Chaiyaphum, 600 m alt., fr. Feb., *K. Larsen et al.* 31813 (AAU).

**12. *Cladopus fallax*** C. Cusset in Fl. Cambodge, Laos, Vietnam 14: 72, pl. 10, f. 10, 11, 1973 (Fig. 13). *Typus*: Massif du Lang Biang entre Klou et Da Nhim, Tuyên Doc, southern Vietnam, *Chevalier* 30946a (P!).

*Cladopus nymanii* auct. (non H. Möller); C. Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 14(1): 22, f. 2, 4-7, 1992, p.p.

Root creeping, adhering to rock surface, ribbon-like (apparently amorphous when old), 2-2.5 mm wide, monopodially or anisotomously branched, with tufts of leaves near edge on both flanks of root at all branch points; leaves to 5 per tuft, linear, flat, obtuse, to 1.7 mm long. Flowering shoot very short; bracts 4-6, in two ranks, digitately divided, lobes 4-6, oblong, ca. 0.5 mm × 0.2 mm, hardly rough particularly when fresh; flower 1, peduncle ca. 1.5 mm long, bud covered by spathe, spathe



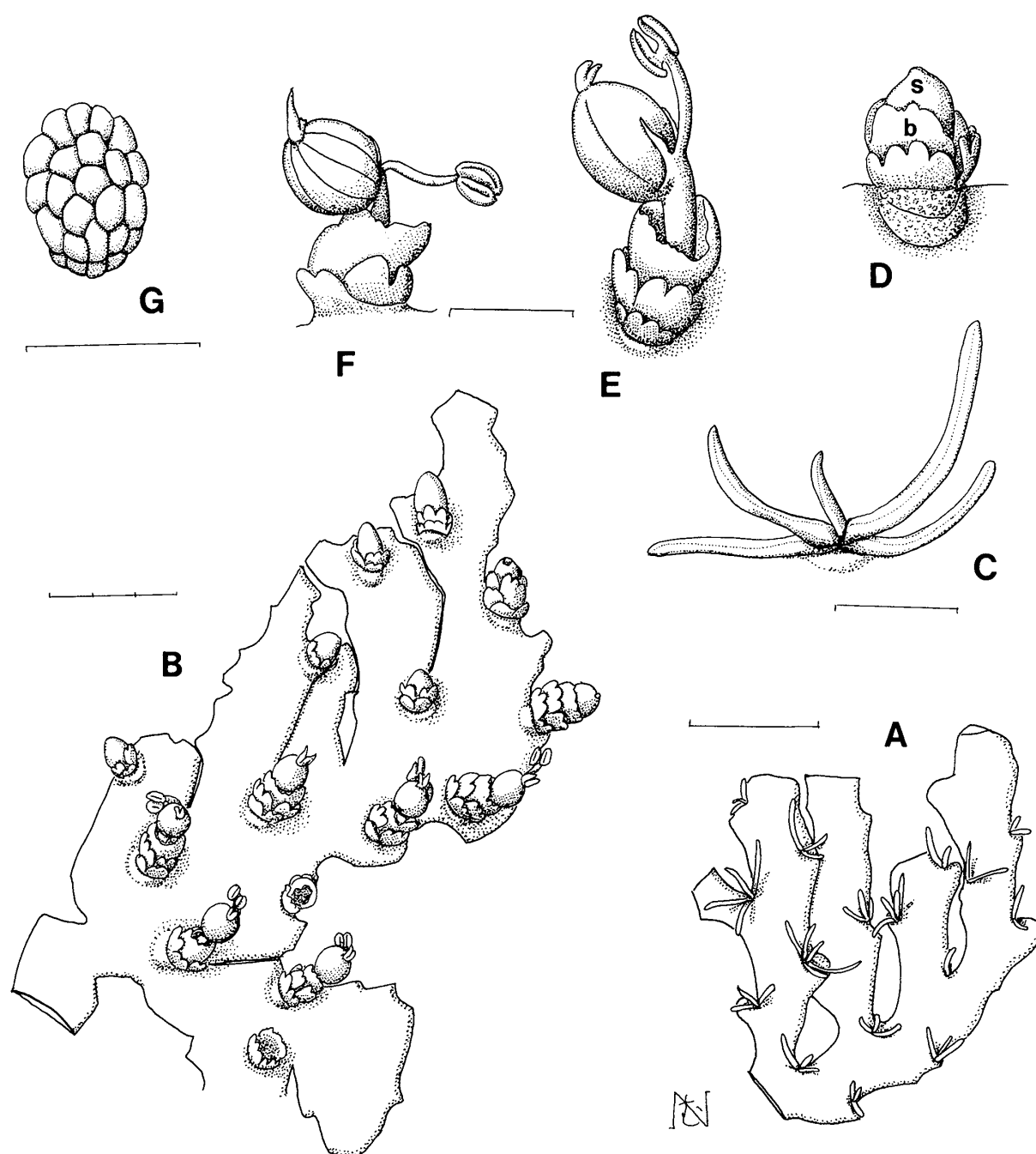


FIG. 12. *Cladopus taiensis* (A, C, M. Kato et al. TL-101; B, D-G, M. Kato et al. TL-302). A, B, Vegetative (A) and reproductive (B) roots. C. Tuft of leaves. D. Flower bud covered by spathe (s) above bract (b). E. Flower at anthesis. F. Young fruit. G. Ovules on ovary septum (not seen). Scale bars = 5 mm for A; 3 mm for B; 1 mm for C-G.

globose, submucronate, irregularly ruptured near apex at anthesis; tepals 2, 1 on each side of stamen, linear, 1-1.5 mm long; stamen 1, to 1.5 mm long, longer than ovary; ovary globose-ellipsoid, 1-1.2 mm long, ca. 1 mm thick, 2-locular, with 2 nearly

vertical grooves; septum hemispherical in central part, margins membranaceous; stigmas 2, forked near base, ca. 0.5 mm long, linear to subulate, entire, procumbent; ovules covering entire septum surface, 10-20 per locule. Capsule stalked (stalk to

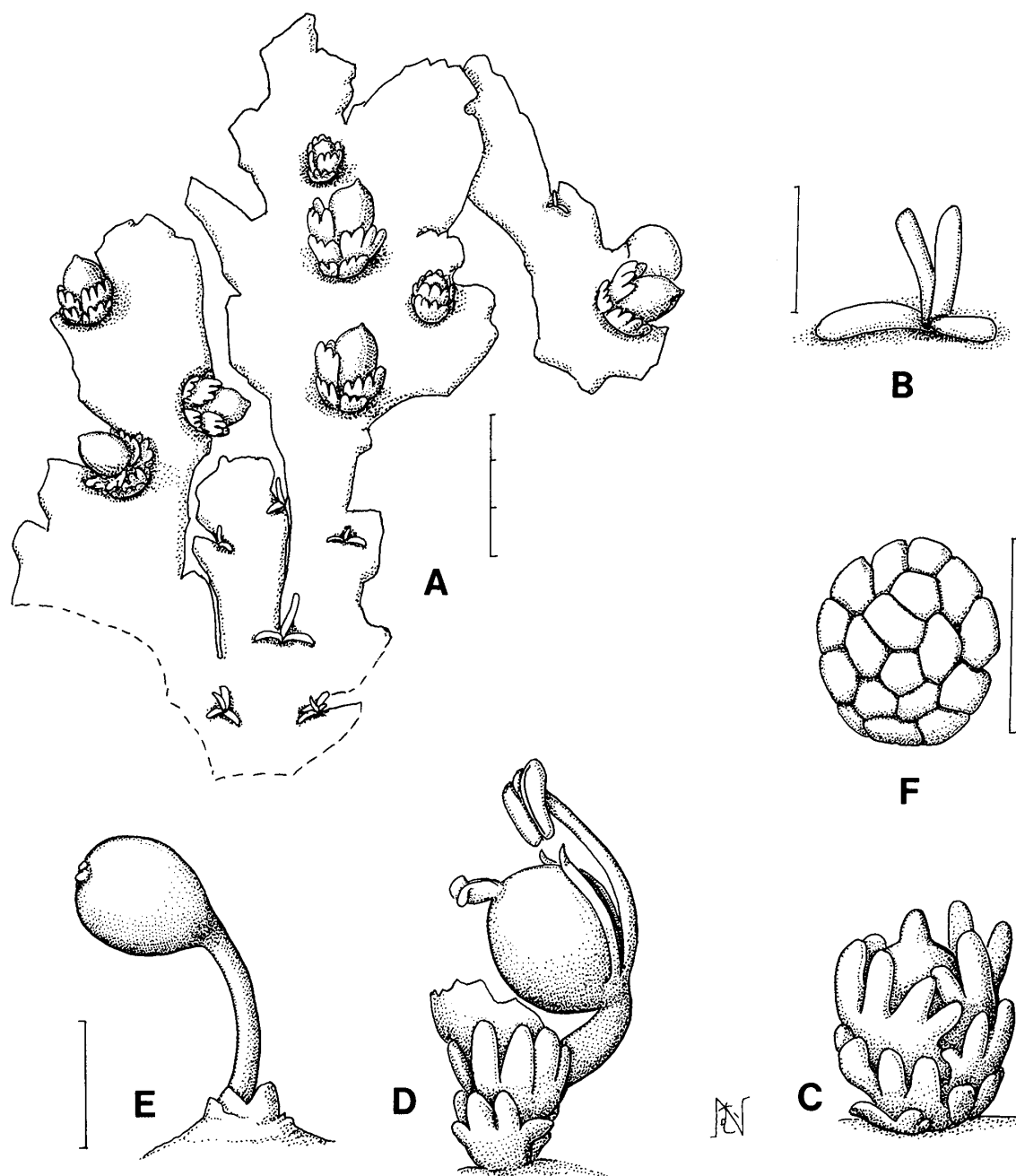


FIG. 13. *Cladopus fallax* (M. Kato & T. Wongprasert TL-701, type). A. Tufts of leaves and young flowering shoots on dorsal surface of old, ribbon-like root with irregular lobes at margin. B. Tuft of leaves. C. Flower bud covered by spathe above digitate bracts. D. Flower at anthesis extruding from ruptured spathe. E. Stalked fruit. F. Ovules on ovary septum (not seen). Scales bars = 3 mm for A; 1 mm for B-F.

1.7 mm long), globose, 1.5 mm long, smooth.

*Distribution.* Thailand (southeastern), southern Vietnam.

*Notes.* This is the first report of *Cladopus fallax* from Thailand. The species was originally

described from southern Vietnam by Cusset (1972). A specimen (Sørensen *et al.* 429) collected from Soi Dao was identified as *Cladopus nymanii* (Royaen 1965) or *C. taiensis* (Cusset 1992), but probably is referable here.

Cusset (1992) reduced *Cladopus fallax* to a synonym of *C. nymanii* in the very broad sense including local species of China and Japan, as noted above. That treatment resulted in a variable and widely distributed *C. nymanii*; however, molecular evidence refutes Cusset's (1992) lumping (Kita & Kato 2001, 2004a). *Cladopus fallax* is most closely related to *C. taiensis* (Y. Kita unpubl. data). Morphologically, *C. fallax* differs considerably from *C. nymanii* in that the root is up to 2.5 mm wide (vs. to 5 mm in *C. nymanii* sensu stricto, the stamen is up to 1.5 mm long (vs. 2.5 mm), and the ovules are 10-20 per locule (vs. up to 50) (Kato & Hambali 2001). *Cladopus fallax* is also distinct from *C. taiensis* in the digitate bracts with lobes thick and somewhat rough on the surface.

*Other specimens examined:* Southeastern: Nam Tok Wang Kaphrae waterfall, Khao Soi Dao Wildlife Sanctuary, Pong Ram Non Dist., Chanthaburi, 12°58'N, 102°14'E, 260 m alt., fr. Mar., *P. Phonsena* 3299, *M. Kato* & *T. Wongprasert* TL-701.

### **Polypleurum** (Taylor ex Tul.) Warm.

Danske Vidensk. Selsk. Skrift. ser. 6, Nat. Math. 11(1): 4, 56, 64, 1901; Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 14(1): 36, 1992; Mathew & Satheesh, Aquat. Bot. 57: 257, 1997 - *Dicraeia* Thou. sect. *Polypleurum* Taylor ex Tul., Arch. Mus. Paris 6: 118, 1852 - *Podostemum* Michx. sect. *Polypleurum* (Taylor ex Tul.) Benth. & Hook. f., Gen. Pl. 3: 112, 1880, excl. *Mniopsis* Mart. & Zucc. sect. *Griffithella* Tul. et *Hydrobryum* Endl. sect. *Zeylanidium* Tul. *Typus:* *Polypleurum wallichii* (R. Br. ex Griff.) Warm.

*Polypleurella* Engl., Beibl. Bot. Jahrb. 61(138): 9, 1927; Nat. Pflanzenfam. 18a: 48, 1930; Cook, Aquat. Plant Book, 2nd ed. 188, 1996. *Typus:* *Polypleurella schmidtiana* (Warm.) Engl.

Root creeping, adhering to rock surface, flattened, ribbon-like or crustaceous (in *Polypleurum filifolium* (Ramam. & Joseph) Nagendran *et al.* of southern India), branched, with tufts of leaves on both flanks

or on dorsal surface at all branch points, or with long cylindrical shoots (*P. erectum*, *P. longicaule*); leaves linear. Flowering shoot short, bearing 2-6 simple bracts. Flower 1, bud covered by spathella, spathella ellipsoid or elongate, irregularly ruptured near apex at anthesis; peduncle various in length; tepals 2, 1 on each side of stamen, uppermost on peduncle, linear; stamens 1 or 2, when 2 then branched from common andropod; ovary ellipsoid, more or less flattened, 1- or 2-locular; ovules borne on septum surface or on reduced marginal surface of septum; stigmas 2, equal; capsule stalked, ellipsoid, more or less flattened, ribs 8-13 or inconspicuous, 2-valved. Species 15, 9 in Thailand.

*Distribution:* Thailand, Laos, Myanmar, northern and southern India, Sri Lanka.

*Notes:* Among the Asian genera of Podostemoideae, *Polypleurum* is distinguished from *Cladopus* and *Paracladopus* in the more or less flattened, ellipsoid, rough capsule with longitudinal ribs and from *Hanseniella*, *Hydrobryum* and *Thawatchaia* in the ribbon-like root. *Polypleurum* has been characterized by the unequal valves of the ovaries and the 8 capsule ribs (Cusset 1992), but the capsule ribs are variable, ranging from 8 to 15 in several species from Thailand. *Polypleurum* of Thailand, as in India and Sri Lanka, except for *P. filifolium* with crustaceous roots (Cusset 1992), has ribbon-like roots. It is likely that the crustaceous roots are derived independently in *P. filifolium*; *Hanseniella*, *Hydrobryum* and *Thawatchaia* of the *Cladopus-Hydrobryum* clade; and a group of *Zeylanidium maheshwarii* and *Z. olivaceum* (Gardner) Engl. (Kita & Kato 2001, Suzuki *et al.* 2002). In Africa, too, there are other Podostemaceae (e.g., *Ledermannia*) with crustaceous roots (Cusset 1987), suggesting convergences.

*Polypleurum* is distributed from Sri Lanka and India (northern and southern) east to Thailand and Laos (Cusset 1992, Kato & Fukuoka 2002, present study). Among the seven species recognized by Cusset (1992), *P. munnarensis* Nagendran & Arekal,

*P. filifolium*, and *P. dichotomum* (Gardner) J.B.Hall are endemic to southern India, *P. elongatum* (Gardner) J. B. Hall is endemic to Sri Lanka, and *P. stylosum* is in Sri Lanka and southern India. Two recently described species, *P. prostratum* C. J. Mathew & Nileena and *P. disciforme* C. J. Mathew & Nileena, are in southern India (Mathew *et al.* 2003). *Polypleurum wallichii* occurs widely from India through Laos (Kato & Fukuoka 2002), and the remaining *P. schmidtianum* and 8 new species occur in Thailand, except on the peninsular.

All Sri Lankan and Indian species of *Polypleurum* including *P. wallichii*, the type of the genus *Polypleurum*, are characterized by the 2 stamens and 8 capsule ribs, while all species of Thailand have a single stamen (except for *P. wallichii*) and 8-15 ribs. *Polypleurum stylosum* shares with *P. wallichii* the very broadly ribbon-like roots, the tufts of leaves on the flanks between the root branches and the 2 stamens. Of the species in Thailand, *P. wallichii*, along with the extra-Thai *P. stylosum* and *P. elongatum*, forms one of two clades; all other species examined are in a second clade (Kita & Kato 2001, Y. Kita unpubl. data). The latter clade may be called *Polypleurella* at an infrageneric rank, if an infrageneric classification is proposed. The genus *Polypleurella* was established for *P. schmidtiana* of Thailand which has a single stamen (Engler 1927), but it was reduced to a synonym of *Polypleurum* by Cusset (1992). The clade may be divided into two, i.e., a group of *P. longistylousum* and *P. schmidtianum*, defined by the tufts of leaves borne on the sides of the root between the root branches, the solitary stamen and the capsule ribs 8-12, while a group including *P. wongprasertii* and others is characterized by the shoots or tufts of leaves borne exclusively at the branch points of the roots, the solitary stamens, and the capsule ribs 10-15. This classification may be consistent with a molecular phylogeny in which *P. longistylousum* is basal in the clade of Thai *Polypleurum*, excluding *P. wallichii* (Y. Kita unpubl. res.), although *P. schmidtianum*

was not sequenced. Further molecular and morphological comparison with *P. schmidtianum* and *Diplobryum*, particularly *D. ramosum* and *D. koyamae*, is necessary to determine the infrageneric and generic level systematics of *Polypleurum*.

Regular association of tufts of leaves (shoots) with root branching occurs elsewhere in *Cladopus*, *Zeylanidium subulatum*, and *Z. lichenoides* (Rutishauser 1997, Mathew & Satheesh 1997, Jäger-Zürn 2000), as well as in many species of *Polypleurum*. Hiyama *et al.* (2002) and Koi & Kato (2003) showed in the two species of *Zeylanidium* and *Cladopus javanicus*, respectively, that the initiation and development of a shoot occurs in the root apical meristem, resulting in division into two unequal meristems that give rise to an anisotomous branching of the root. A similar developmental mechanism may be underlain in *Polypleurum*.

**13. *Polypleurum wallichii*** (R. Br. ex Griff.) Warm., Danske Vidensk. Selsk. Skrift., ser. 6, Nat. Math. 11(1): 57, 1901; Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 14(1): 42, f. 8, 1992; Raveendran & Mathew, Rheede 2: 106, f. 1, 1994 - *Podostemum wallichii* R. Br. ex Griff., Asiatic Res. 19: 103, tab. 17, 1836 - *Dicraea wallichii* (R.Br. ex Griff.) Tul., Ann. Sci. Nat. ser. 3, 11: 101, 1849; Willis, Ann. Roy. Bot. Gard. Peradeniya 1: 223, 1902. *Typus*: Cherrapunji, India, Griffith s.n. (K!).

*Dicraea minor* Wedd., in DC., Prodr. 17: 71, 1873; Willis, Ann. Roy. Bot. Gard. Peradeniya 1: 223, 1902 - *Podostemum minor* (Wedd.) Benth., in Benth. & Hook. f., Gen. Pl. 3: 112, 1880; Hook. f., Fl. Brit. Ind. 5: 67, 1886 - *Polypleurum minor* (Wedd.) Nagendran, Arekal & Subramanyan, Plant Syst. Evol. 128: 217, 1977. *Typus*: Mts. Khasi, India, Griffith 2437 (holo K!; iso P).

*Dicraea wallichii* (R. Br. ex Griff.) Tul. var.  *khasiana* Willis, Ann. Roy. Bot. Gard. Peradeniya 1: 224, 1902. *Syntypus*: Maomloo River, Cherrapunji; Wallich, Sylhet rivers; Gomez, Sylhet Mts., Griffith,

*Hooker, Clarke, Willis* (C!).

*Dicraea wallichii* (R. Br. ex Griff.) Tul. var. *striata* Willis, Ann. Roy. Bot. Gard. Peradeniya 1: 225, 1902. *Syntypus*: Moulmen, Myanmar, *Lehmann* 3, *Wallich* 33, *Parish* s.n. (K!).

**13a. var. wallichii** (Fig. 14)

Root attached to rock by base, distally free, floating, ribbon-like, to 5 mm wide, ca. 1 mm thick, irregularly and often branched, with tufts of leaves on dorsal surface near margins, not associated with root branching; leaves few per tuft, linear-oblong, dorsiventrally flattened, apex obtuse, to 5(-10) mm long. Flowering shoots on both flanks of roots; bracts 4, lanceolate to ovate-lanceolate, acute or acuminate, apex often caducous; flower 1, bud covered by spathe, spathe 2-4 mm long, ruptured near apex at anthesis; peduncle 5-8 mm long; tepals 2, 1 on each side of stamen, to 1 mm long; stamens 2, branched below apex, as long as ovary or slightly longer, 2.5-3 mm long, anthers caducous; ovary ellipsoid, slightly flattened, to 2.5 mm long; stigmas 2, equal, forked at base, lanceolate or boat-like, to 0.8 mm long, each often bifid; ovules covering entire septum surface, 40-50 per locule; capsule ribs 8-9.

*Distribution*: Thailand (northern, central, eastern), northern and southern India, Myanmar, Laos.

*Notes*: *Polypleurum wallichii* is the widest and northernmost in distribution in *Polypleurum*, but also occurs disjunctly in Kerala, southern India (Raveendran & Mathew 1994). A molecular phylogeny shows that, among two Sri Lankan species and all species from Thailand examined, *P. wallichii* is most closely related to the Sri Lankan and southern Indian *P. stylosum*, which has similar ribbon-like, floating roots and 2-4 bracts, and next most closely related to the Sri Lankan *P. elongatum*, which also has long, floating roots and 2-4 bracts (Kita & Kato 2001, Y. Kita unpubl. data). Characters shared by the three species, i.e., more or less floating roots, tufts of leaves borne between root branch-

es, and 2 forked stamens, reflect their close relationships.

*Other specimens examined*: Central: Orchid Falls, Khao Yai Natl. Park, 700 m alt., fl. Oct., fr. Nov., *Charoenphol et al.* 4366 (BKF, E, K, L, P), *Hennipman* 4001 (BKF, K, L, P), *C. Chermisrivathana* 618 (BK); Pha Kluaimai waterfalls and Haew Suwat waterfalls, Khao Yai Natl. Park, Nakawn Nayok, 700 m alt., fl. fr. Jan., *M. Kato et al.* TL-55, TL-56; Suwat waterfall, Khao Yai Natl. Park, 650 m alt., *Lambinon* 87/81 (AAU); Khao Yai Natl. Park, ca. 800 m alt., fl. Feb., *T. Smitinand* 8631 (BKF, C, L); Nakhon Nayok, Khao Yai Natl. Park, 800 m alt., fl. fr. Nov., *T. Smitinand & Robbins* 7875 (C); Khao Yai Natl. Park, fl. fr. Jan., *T. Smitinand* 8632; Khao Yai Natl. Park, prov. Saraburi, 800 m alt., fr. Dec., *Vidal* 4620 (P); Nang Rong waterfalls, Khao Yai Natl. Park, 14°20'N, 101°19'E, 50 m alt., st. Sep., fl.-buds, fl. Nov., fl. fr. Dec., *M. Kato et al.* TL-201, TL-303, *M. Kato & T. Wongprasert* TL-601, TL-602; Wang Takrai waterfalls, 14°20'N, 101°18'E, 50 m alt., fl. fr. Dec., *M. Kato et al.* TL-301; Sarika waterfalls, 14°18'N, 101°15'E, 100 m alt., fl. fr. Dec., *M. Kato et al.* TL-305, 22 Dec. 1988, *P. Cribb* s.n. (K). Eastern: Huaychan waterfall, Khoonharn Dist., Si Sa Ket, *Somran Suddee* s.n., 23 Nov. 2004. Northern: Doi Saket, Chiang Mai, fr., *T. Smitinand & G. Seidenfaden* s.n. (C).

**13b. var. parvum** M. Kato, **var. nov.** (Fig. 15)

A var. *wallichii* radicibus angustis, foliis brevibus et floribus parvis differt.

*Typus*: Haew Narok waterfalls, Khao Yai Natl. Park, Central Thailand, 14°17'N, 101°23'E, 400 m alt., Dec. 2000 (fl.), *M. Kato, Y. Kita & T. Wongprasert* TL-308 (holo BKF, iso TI, TNS).

Root ribbon-like, to 3 mm wide, irregularly and often branched, with tufts of leaves near sides, not associated with root branching; leaves 1 or 2 per tuft, linear, to 2.5 mm long. Flowering shoots on both flanks of root; bracts 4, lanceolate to ovate-lanceolate, apex acute or obtuse; flower 1, bud covered by spathe, spathe ruptured near apex at anthesis; peduncle 2-4 mm long; tepals 2, 1 on each side of stamen; stamens 2, branched below apex, as long as pistil (including stigma) or longer, 1.5-2 mm long, anthers caducous; ovary 2-locular, ellipsoid, slight-

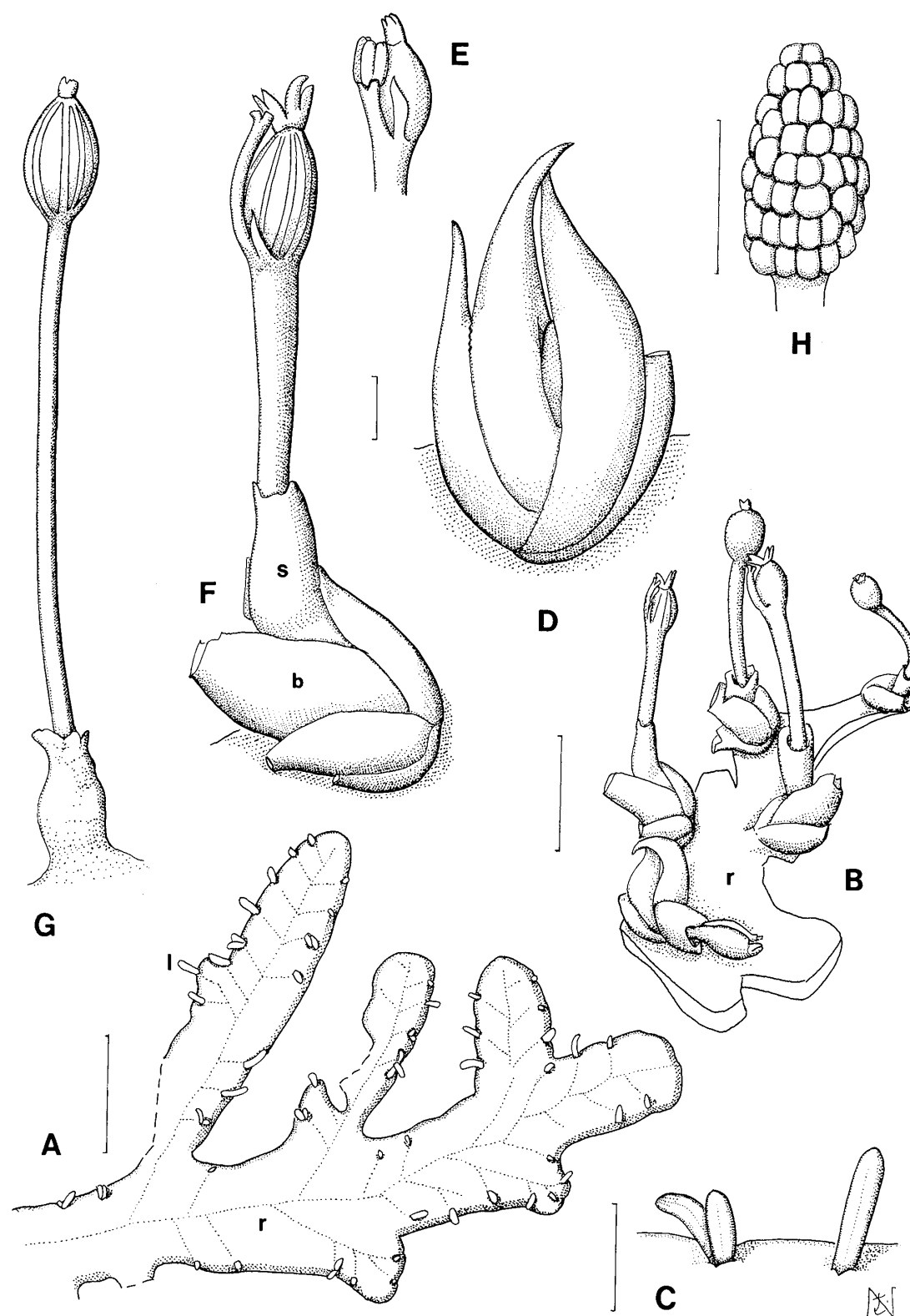


FIG. 14. *Polypleurum wallichii* var. *wallichii* (A, C, M. Kato & T. Wongprasert TL-601; B, D-H, M. Kato et al. TL-305). A, B. Vegetative (A) root (*r*) with leaves (*l*) near flanks and reproductive (B) root with flowering shoots near flanks. C. One and two leaves protruding from root. D. Flower bud subtended by bracts. E. Young flower. F. Flower protruding from ruptured spathe (*s*) above bracts (*b*) at anthesis. Note that anthers have fallen. G. Stalked fruit. H. Ovules on ovary septum. Scale bars = 5 mm for A, B; 1 mm for C-H.

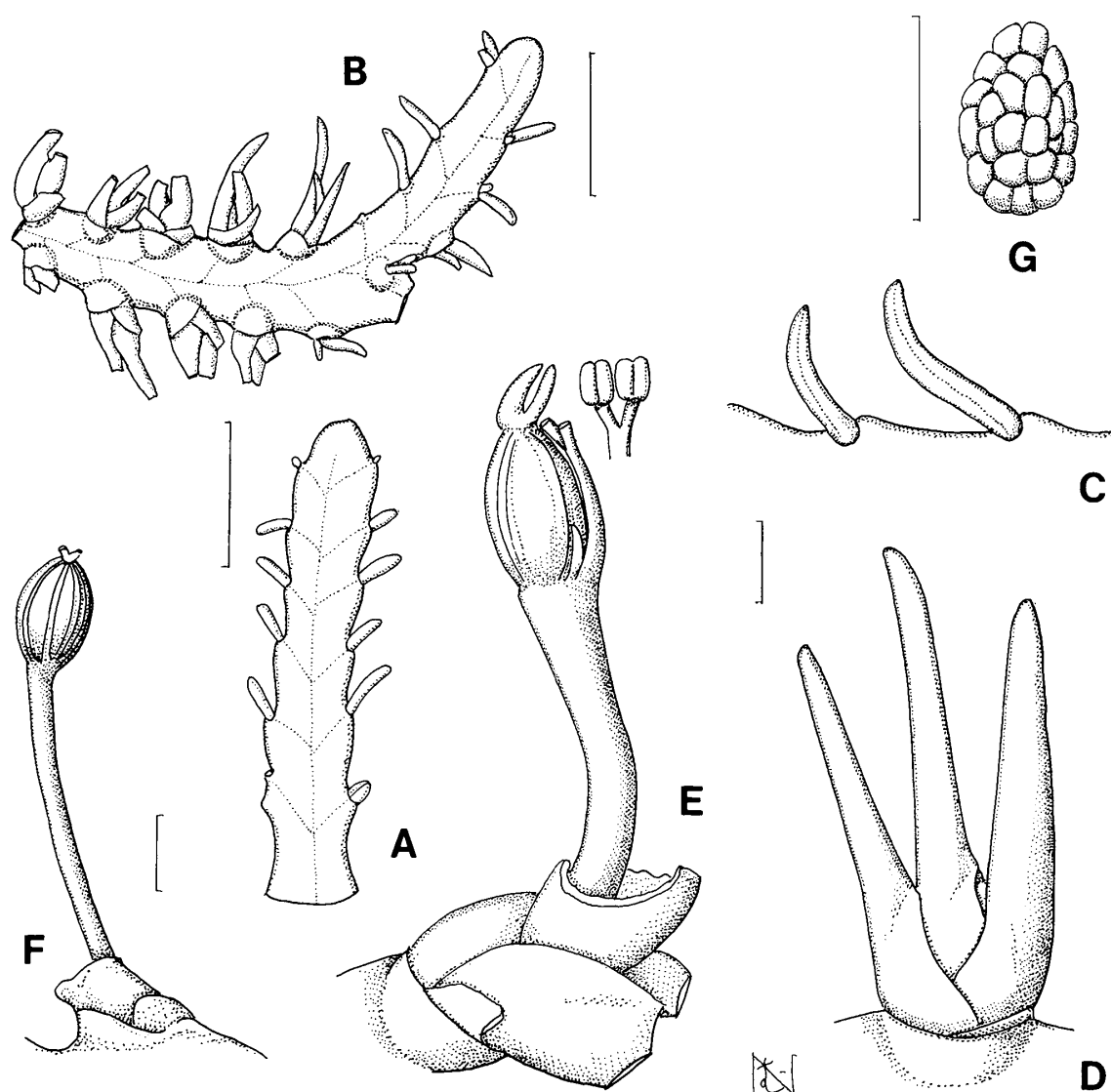


FIG. 15. *Polypleurum wallichii* var. *parvum* (A-F, M. Kato et al. TL-308, type; G, Kita & T. Wongprasert TL-402). A, B. Vegetative (A) and reproductive (B) roots. C. Leaves near flank of root. D. Bracts subtending flower bud. E. Flower extruding from ruptured spathe above bracts at anthesis. Anthers have fallen and distal portion of stamen is illustrated. F. Stalked fruit. G. Ovules on ovary septum. Scale bars = 5 mm for A, B; 1 mm for C-G.

ly flattened, 1.2-1.5 mm long; stigmas 2, equal, forked at base, lanceolate or boat-like, 0.4-0.5 mm long; ovules covering entire septum surface, 25-45 per locule; capsule ribs 8.

*Distribution:* Thailand (central).

*Notes:* *Polypleurum wallichii* var. *parvum* differs from var. *wallichii* in its smaller size, narrower root (to 3 mm wide vs. to 5 mm wide in var. *wallichii*), shorter leaf (to 2.5 mm long vs. to 5(-10) mm

long), and smaller flowers (e.g., peduncle 2-4 mm long vs. 5-8 mm long, ovary 1.2-1.5 mm long vs. to 2.5 mm long).

Var. *parvum* differs from *Polypleurum minor* (= *P. wallichii* var. *wallichii*; Griffith 2427) in the narrower root (vs. 3-10 mm wide in *P. minor*), while it is similar in the short peduncle (vs. 1-4 mm long in *P. minor*) (Willis 1902a). Willis (1902a) considered that the imperfectly known *P. minor* may be a

dwarf phase of *P. wallichii*.

*Other specimens examined:* Central: Haew Narok waterfalls, Khao Yai Natl. Park, Central Thailand, 400 m alt., fl. fr. Dec., Jan., *M. Kato et al. TL-61, Kita & T. Wongprasert TL-402*; Administration Center, Khao Yai Natl. Park, 780 m alt., fr. Mar., *Lambinon 87/65 (AAU)*.

**14. *Polypleurum schmidtianum*** Warm. in Johs. Schmidt, Bot. Tidsskr. 24(3): 258, 1901; Danske Vidensk. Selsk. Skrift. ser. 6. Nat. Math. 11(1): 3, f. 1-6, 1901; Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 14(1): 38, 1992—*Polypleurella schmidtiana* (Warm.) Engl., Bot. Jahrb. Syst. 61: 9, 1927; Royen, Dansk Bot. Ark. 23: 185, 1965. *Typus:* Klong Sarlakpet, Koh Chang, 600 ft, Southeastern Thailand (fl. fr. Mar.), *Schmidt s.n. (C 3160, not seen) (C)*.

Root ribbon-like, 2-4 mm wide, irregularly and often branched, with tufts of leaves near both sides, not associated with root branching; leaves 2-4 per tuft, in 2 ranks, linear, 1.5-3(-6) mm long, 0.2-0.4 mm wide. Flowering shoots on both flanks of root; bracts 3-4(-6), in 2 ranks, 2-3 mm long, sheathed, with perpendicularly wide, prominent sheath-like base surrounding flower bud, not papillate, distally linear; flower 1, bud covered by ellipsoid spathella, spathella not papillate, ruptured near apex at anthesis, ruptured spathella 1.5-2 mm long; peduncle 6-7 mm long; tepals 2, 1 on each side of stamen, 0.5-0.7 mm long; stamen 1, as long as ovary or longer, 1.2 mm long; ovary 2-locular, ellipsoid, slightly flattened, 1.2-1.5 mm long, ca. 0.7 mm wide; stigmas 2 (or 3), subequal, forked at base, linear-deltoid, narrowed to apex, 0.2-0.4 mm long; ovules covering entire septum surface, 25-35 per locule; capsule stalked (6-12 mm long), ribs 8.

*Distribution:* Thailand (southeastern, central [Cusset 1992]).

*Notes:* This species occurs in Saphan Hin waterfall SW of Trat and Ko Chang. *Charoenphol et al. 5115* from the adjacent Ko Kut, which was identified as *P. schmidtianum* by Cusset (1992), is

referred to *P. wongprasertii*. Cusset (1992) cited additional collections from Nakhon Nayok (Khao Yai National Park) in central Thailand, but I did not collect *P. schmidtianum* in the area.

This species is most similar to *Polypleurum longistylosum* in the arrangement of the tufts of leaves on the flanks of the root between branches and the solitary stamens, bud differs in the length of the peduncle (6-7 mm vs. 1 mm) and the length (0.2-0.4 mm vs. 1-1.2 mm) and number (2 [or 3]) of stigmas, and number of ovary locules (2 vs. 1), ovules (25-35 vs. 10-15) and capsule ribs (8 vs. 10-12). It is also similar to *P. wallichii* in the broad root and the aforementioned arrangement of leaf tufts, but differs in the single stamen. Moreover, *P. schmidtianum* differs from all congeners in the perpendicularly wide bracts with basal sheaths and needle-like distal tips.

*Other specimens examined:* Southeastern: Saphan Hin waterfall, Trat, 12°06'N, 102°42'E, 40 m alt., fl. Dec., Jan., *R. Imaichi et al. TIK-22, 23, M. Kato et al. TL-1508*; Tharn Mayom waterfall, Ko Chang, 12°21'N, 102°21'E, 200 m alt., st. Jan., *M. Kato et al. TL-1527*.

**15. *Polypleurum longistylosum*** M. Kato, *sp. nov.* (Fig. 16)

*P. schmidtianum* staminibus singularibus simile, surculis utrinque inter ramos radicum multis, sed ovariois unilocularibus, stylis plus stigmatibus longis difert.

*Typus:* Huay Luang waterfalls, Phu Chong Nayoi Natl. Park, Ubon Ratchathani, Eastern Thailand, 14°27'N, 105°16'E, 300 m alt., Dec. 27, 2000 (fl. fr.), *M. Kato, Y. Kita & T. Wongprasert TL-318* (holo BKF, iso TI, TNS).

Root ribbon-like, rarely branched, 1-1.5(-2) mm wide, with tufts of leaves on both flanks, not associated with root branching, 2-4 mm apart; leaves 4-8 per tuft, in 2 ranks, to 5 mm long, needle-like. Flowering shoots on both flanks of root, very short; bracts to 6, needle-like, to 4 mm long; flower 1, bud covered by ellipsoid spathella, spathella papillate,



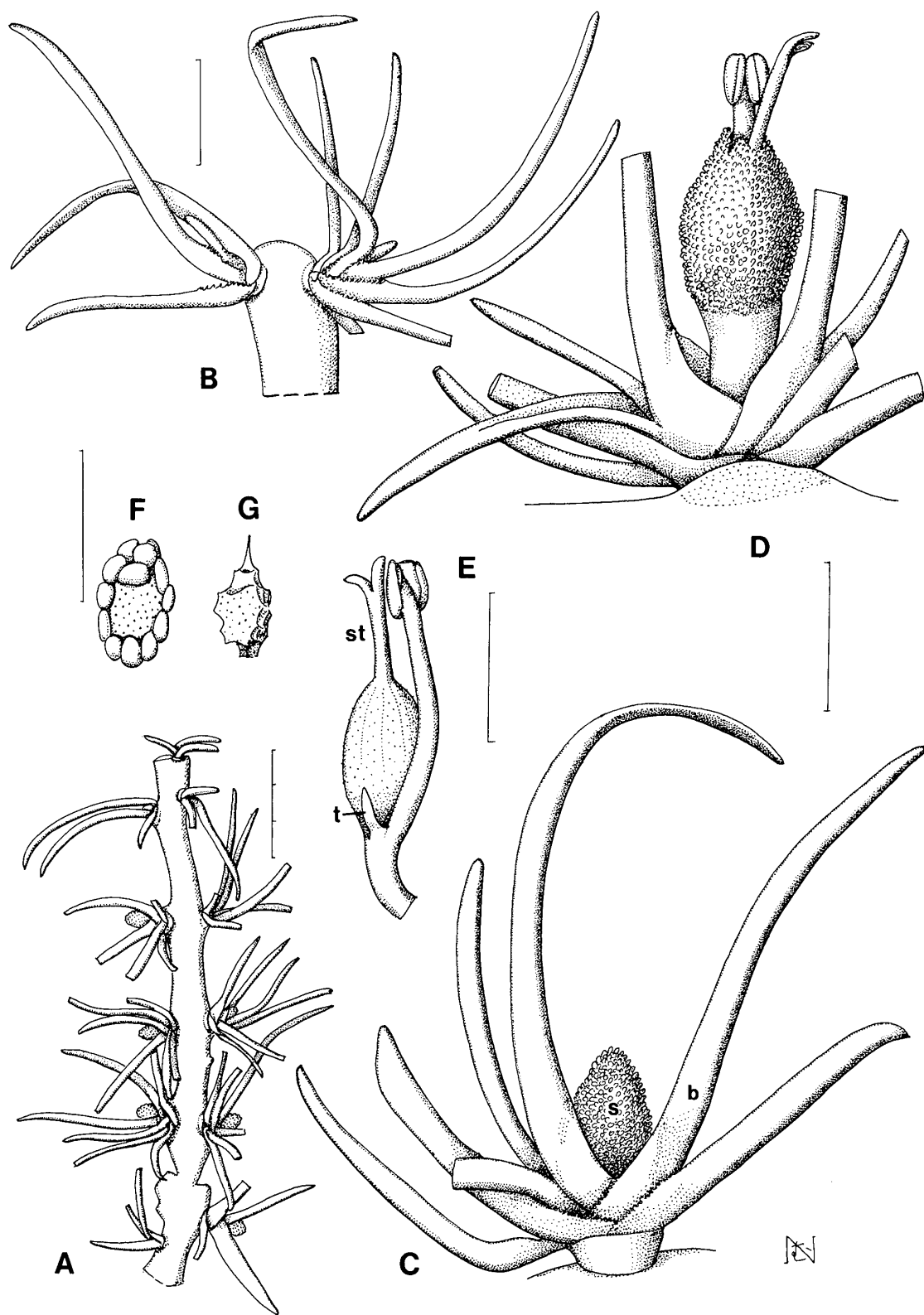


FIG. 16. *Polypleurum longistylusum* (Kato et al. TL-318, type). A. Ribbon-like root with tufts of leaves and young flowering shoots on flanks. B. Tufts of leaves on flanks of root. C. Flower bud covered by spathe (*s*) above bracts (*b*). D. Flower above bracts at anthesis with ovary covered by spathe. E. Flower with spathe removed, showing tepal (*t*), stamen, and ovary with style plus stigma (*st*) on top. F. Ovules on ovary septum with sterile central portion. G. Ovary septum without thin margin. Scale bars = 3 mm for A; 1 mm for B-G.

ruptured near apex at anthesis, persistent, enclosing ovary and lower half of stigma; peduncle to 1 mm long; tepals 2, 1 on each side of stamen, linear, 0.2 mm long; stamen 1, to 1.7 mm long, protruding from spathella; ovary dark brown, ellipsoid, ca. 1 mm long, 1-locular (septum except distal and proximal ends free from ovary wall), placentation pseudo-central; stigmas (s.l., i.e., style and two stigmas) thin, needle-like, 1-1.2 mm long, as long as ovary or longer, branched above or at middle, upper half exserted from spathella; ovules on marginal surface of septum, 10-15 per septum; capsule ribs 10-12, inconspicuous.

*Distribution:* Thailand (eastern).

*Notes:* *Polypleurum longistylosum* is similar to all species of *Polypleurum* except *P. stylosum* and *P. wallichii* in having a single stamen, but differs from all Thai species in the ovaries and stamens being nearly completely enclosed in the spathella at anthesis, style + stigma as long as ovary and branched at or above middle, ovary 1-locular (placentation pseudo-central), ovules on the marginal surface of the septum, and capsule ribs 10-12 and inconspicuous. The species is similar to both *P. schmidtianum* and *P. wallichii* in that the tufts of leaves and flowering shoots are borne along the flanks of the root between the branches. In addition to the above characters, however, it differs from those two species in the narrower root (1-1.5 mm vs. 2-6 mm). *Polypleurum longistylosum* and *P. wallichii* belong to two different clades (Y. Kita unpubl. data). The clade to which *P. longistylosum* belongs includes all species of *Polypleurum* with single stamens and tufts of leaves and flowering shoots borne at the root branching points.

*Other specimens examined:* Eastern: Huay Luang waterfalls, Phu Chong Nayoi Natl. Park, Ubon Ratchathani, 300 m alt., fl. Dec., Y. Kita & T. Wongprasert TL-408; Kaeng Silathip, Phuchong Nayoi Natl. Park, Ubon Ratchathani, fl. Nov., Somran Suddee 2615; Phoolaor waterfall, Si Sa Ket, 14°27'N, 104°39'E, 180 m alt., fl. M. Kato et al. TL-1503.

**16. *Polypleurum wongprasertii* M. Kato, sp. nov.** (Fig. 17)

A *P. wallichio*, *P. schmidtiano* et *P. longistyloso* foliis supra radicibus ad omnem ramificationem, a *P. wallichio* staminibus singularibus, bracteis acuminatis, a *P. erectis* et *P. longicauli* floribus subsessilibus, a *P. rubroradicansi* atrobrunneis, angustis differt.

*Typus:* Huay Luang waterfalls, Phu Chong Nayoi Natl. Park, Ubon Ratchathani, Eastern Thailand, 14°27'N, 105°16'E, 300 m alt., Dec. 28, 2000 (fl. fr.), M. Kato, Y. Kita & T. Wongprasert TL-319 (holo BKF; iso TI, TNS).

Root ribbon-like, (1-)1.5-3 mm wide, branched, with tufts of leaves on dorsal surface exclusively at every root branching point; leaves 2-4 per tuft, 5-15(-20) mm long, base sheath-like, ovate, papillate, persistent, forming a mound around leaves, distal part needle-like, caducous. Flowering shoot on dorsal surface at point of root branching; bracts 2-4(-6), sheath-like, ovate, papillate, or needle-like with sheath-like base; flower 1, bud covered by spathella, spathella ca. 2 mm long, papillate, ruptured near apex and also split longitudinally at anthesis; peduncle 4-7 mm long; tepals 2, 1 on each side of stamen, 0.7-1 mm long; stamen 1, inserted above base of ovary, 1-1.2 mm long, as tall as ovary; ovary 2-locular, ellipsoid, slightly flattened, 1-1.5 mm long; stigmas 2, linear, narrowed to apex, 0.3-0.6 mm long; ovules covering entire septum surface, ca. 30 per locule; capsule stalked (stalk 5-8 mm long), subsymmetric, ribs 10-12.

*Distribution:* Thailand (eastern, southeastern).

*Notes:* *Polypleurum wongprasertii* is closely related to all species of *Polypleurum* of Thailand except for *P. wallichii* (Kita & Kato 2001, Y. Kita unpubl. res.) and is similar in the papillate spathella and single stamen. Among the species with tufts of leaves or shoots borne on the root at the point of branching, *P. wongprasertii* is most similar to *P. longifolium* in the root being 2-3 mm wide, bracts 2-

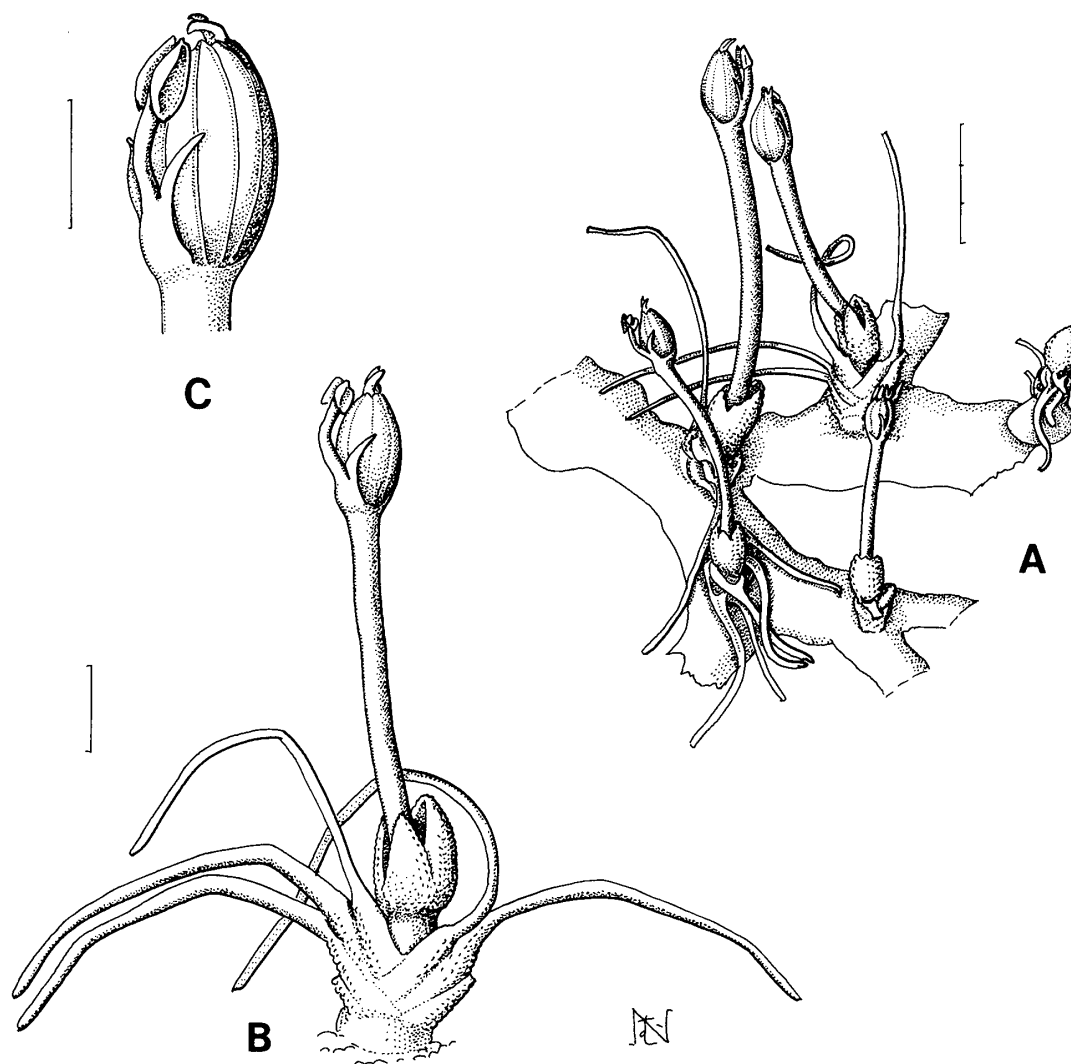


FIG. 17. *Polypleurum wongprasertii* (Kato et al. TL-319, type). A. Ribbon-like root with flowering shoots at branching points. B. Flowering shoot with bracts, spathe, pedunculate flower. C. Flower at anthesis. Scales bars = 3 mm for A; 1 mm for B, C.

4, spathe 2-3 mm long, and peduncle 4-7 mm long. The two species can be discriminated by leaf length, stigma and ovule number (see the key to species). *Polypleurum wongprasertii* is sister to a group of *P. erectum*, *P. longifolium* and *P. phuwaense* (Y. Kita unpubl. data). In the distribution, *P. wongprasertii* is apparently disjunct in Ubon Ratchathani in eastern Thailand and Ko Chang and Ko Kut in southeastern Thailand (see also Notes under *P. schmidtianum*). The plants from the southeastern islands are slightly smaller than those from the eastern area.

*Other specimens examined:* Eastern: Huay Luang

waterfalls, Phu Chong Nayoi Natl. Park, Ubon Ratchathani, 300 m alt., fl. Dec., Y. Kita & T. Wongprasert TL-407; Kaeng Silathip, Phuchong Nayoi Natl. Park, Ubon Ratchathani, fl. Nov., Somran Suddee 2614; Soi Sawan Waterfall, Pha Taem Natl. Park, Ubon Ratchathani, 15°28'N, 105°35'E, 150 m alt., fr. Jan., Feb., Somran Suddee 1738, M. Kato & T. Wongprasert TL-702. Southeastern: Klong Phloo, Ko Chang, fr. Feb., F. Konta & T. Wongprasert s.n., Ko Kut, 12°35'N, 101°31'E, Charoenphol et al. 5115 (AAU, BKF, K).

**17. *Polypleurum longifolium* M. Kato, sp. nov.** (Fig. 18)

*P. erecti*, *P. longicaulis* et *P. wongprasertii* foliis linearibus, longissimis, pedunculis longis, *P. erecti*

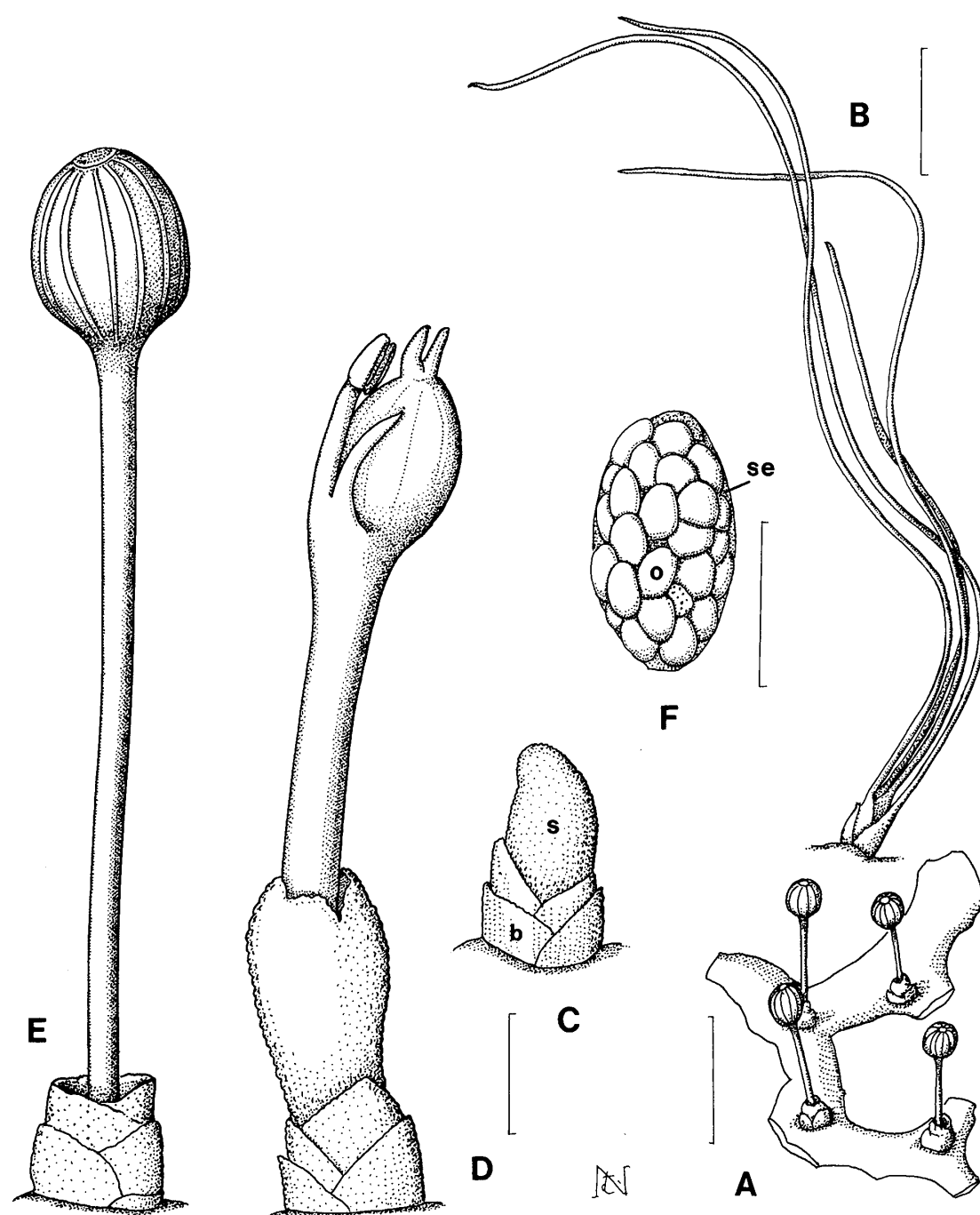


FIG. 18. *Polypleurum longifolium* (A, C-F, M. Kato & T. Wongprasert TL-707, type; B, M. Kato et al. TL-904). A. Ribbon-like root with fruits at branching points. B. Tuft of leaves with sheath-like bases. C. Flower bud covered by spathe (s) above bracts (b). D. Flower at anthesis terminating peduncle. E. Stalked fruit. F. Ovules (o) on ovary septum (se). Scales bars = 5 mm for A, B; 1 mm for C-F.

*ti* bracteis basi vaginiformis, papillatis, distali acicularibus, capsules asymmetricatis simile, sed surculis invisilibus differt.

*Typus*: Cha Naen Waterfall, Phu Wua Wildlife

Sanctuary, Nong Khai, northeastern Thailand, 18°14'N, 103°54'E, 180 m alt., Feb. 25, 2003 (fr.), M. Kato & T. Wongprasert TL-707 (holo BKF, iso TI, TNS).

Root ribbon-like, 2-3 mm wide, isotomously or anisotomously branched, with tufts of leaves (shoots invisible or extremely short) on dorsal surface exclusively at all root branching points; leaves 4-6 per tuft, in 2 ranks, 20-40 mm long, base sheath-like, papillate, distal part needle-like, caducous. Flowering shoots similarly borne on root at root branch points, very short; bracts 2-4, sheath-like, ovate, papillate, with distal portion short or needle-like, 1.5-4 mm long, needles caducous; flower 1, bud covered by spathe, spathe sparsely papillate, 2-3 mm long, split into few valves near apex at anthesis; peduncle 4-7 mm long; tepals 2, 1 on each side of stamen, inserted at apex of peduncle or above base of ovary, linear, 0.7-1 mm long; stamens 1, 1-1.2 mm long, as tall as ovary; ovary 2-locular, ellipsoid, slightly flattened, 1-1.5 mm long; stigmas 2, subdeltoid or deltoid-ovate, 0.2-0.4 mm long; ovules on septum surface except in small lower central area, 18-22 per locule; capsule stalked (stalk 4-7 mm long), asymmetric, 1.5-1.7 mm long, 1-1.2 mm thick, ribs 10-15 including several thin ribs between thick ribs.

*Distribution:* Thailand (northeastern).

*Notes:* *Polypleurum longifolium*, like *P. erectum*, *P. longicaule*, *P. rubroradicans* and *P. wongprasertii*, is unusual in the genus in the leaves being remarkably long (to 4 cm), sheath-like at the base, and needle-like in the distal part. It is most similar to *P. wongprasertii* (for similarities and differences, see Notes under *P. wongprasertii*).

*Other specimen examined:* Northeastern: Cha Naen Waterfall, Phu Wua Wildlife Sanctuary, Nong Khai, st. Dec., M. Kato et al. TL-904.

# **18. *Polypleurum phuwaense* M. Kato, sp. nov.** (Fig. 19)

*P. ubonensi* radicibus taeniformibus, surculis ad omni ramificationibus radice, bracteis acicularibus, spathellis conspicue longis, papillatis, stamine singularibus similissimum, sed bracteis 4-6, spathellis longioribus (usque 4-6 mm), pedunculis usque 10-15 mm longis, ovulis in quoque loculo 15-20 differt.

*Typus:* Chet Si Waterfall, Phu Wua Wildlife Sanctuary, Nong Khai, Northeastern Thailand, 18°10'N, 103°57'E, 210 m alt., Feb. 24, 2003 (fr.), M. Kato & T. Wongprasert TL-705 (holo BKF, iso TI, TNS).

Root ribbon-like, 1.5-3 mm wide, iso- or anisotomously branched (vegetative material lacking). Flowering shoots on dorsal surface at root branching points, no shoots between root branches; bracts 4-6 in 2 ranks, lower ones sheath-like, ovate, papillate, distally subacute (needle-like, caducous?), upper ones 3-5 mm long, needle-like, with papillate sheath-like base, needle smooth; flower 1, at shoot apex, bud covered by spathe, spathe to 4-6 mm long at maturity, papillate, ruptured near apex, split longitudinally at anthesis; peduncle 10-15 mm long; tepals inserted at base of ovary, 1 on each side of stamen, 1-1.5 mm long, slightly shorter than ovary; stamen 1, 1.5-2 mm long, as tall as ovary or slightly taller; ovary 2-locular, ellipsoid, nearly radial, 1.3-1.8 mm long; stigmas 2, linear-deltoid, narrowed to tip, 0.3-0.5 mm long, equal or subequal; ovules on entire septum surface, 15-20 per locule; capsule long stalked (stalk 10-20 mm long), asymmetric, ribs 10-14.

*Distribution:* Thailand (northeastern).

*Notes:* *Polypleurum phuwaense* is similar to *Polypleurum longifolium*, *P. rubroradicans* and *P. wongprasertii* in the ribbon-like roots bearing shoots on the dorsal surface at all branching points, the stem reduced or absent, the bracts sheath-like and papillate basally and needle-like distally, the spathe long and papillate, and the stamen simple. It differs, however, in the bracts being more numerous (4-6; but 2-6 in *P. rubroradicans*) and the longer spathe (4-6 mm), the peduncle very long (10-15 mm), and the ovules slightly fewer (15-20 per locule; but 14-22 in *P. rubroradicans*). In the reduced or absent stem (so that the shoot comprises tufts of leaves), it differs from *P. erectum* and *P. longicaule* with leafy or branched shoots.

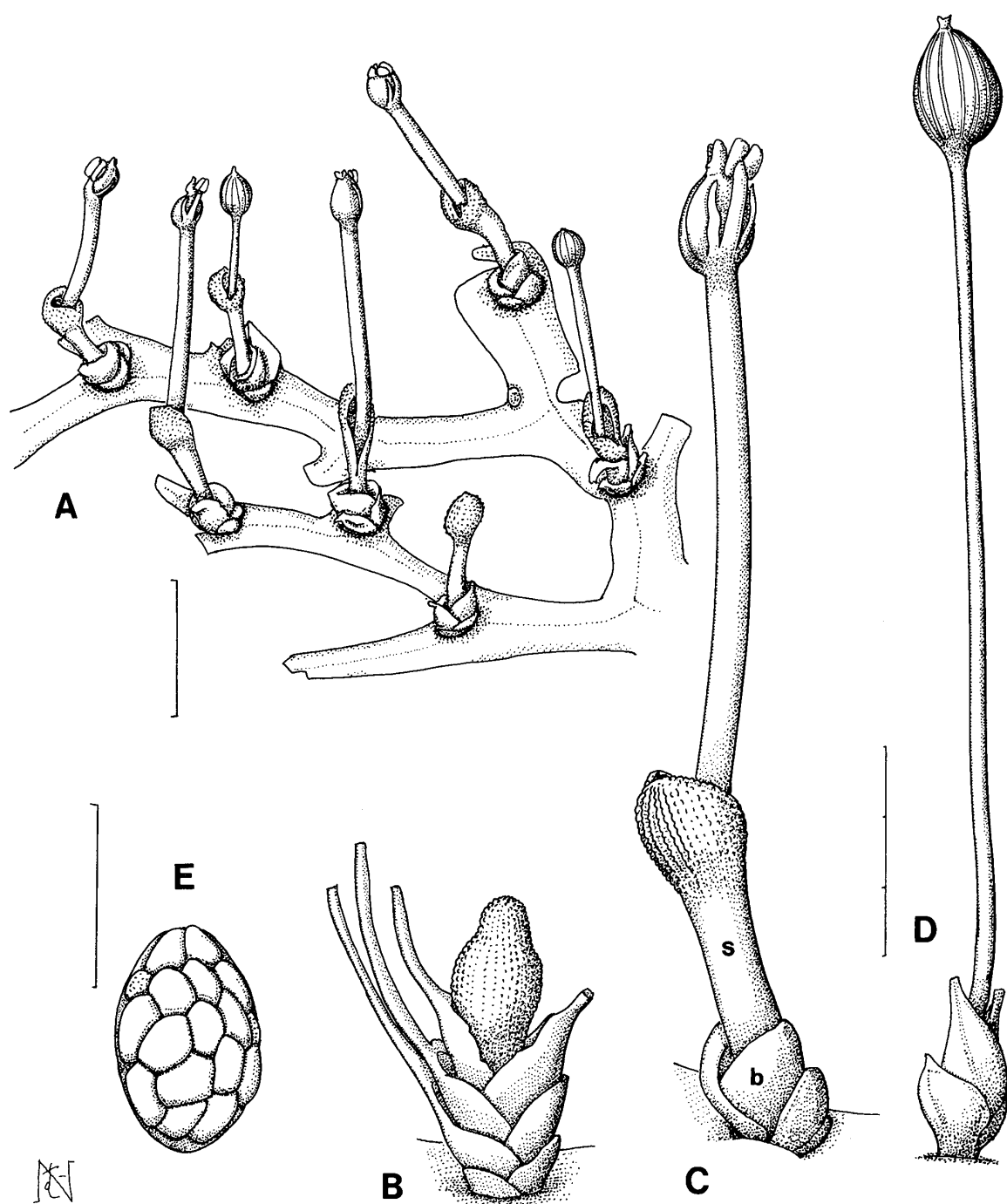


FIG. 19. *Polypleurum phuwaense* (Kato et al. TL-705, type). A. Ribbon-like root with flowering shoots at branching points. B. Flower bud covered by spathe above bracts. C. Flower at anthesis on peduncle with ruptured spathe (s) above bracts (b). D. Stalked fruit. E. Ovules on ovary septum. Scale bars = 5 mm for A; 3 mm for B-D; 1 mm for E.

**19. *Polypleurum rubroradicans* M. Kato, sp. nov.**  
(Fig. 20)

A congeneribus radicibus latisissimis (3-5 mm),  
rubropurpureis, a *P. wallichii*, *P. schmidtiano* et *P.*

*longistyliso* foliis ad ramificationibus radices, a *P.*  
*erectis* et *P. longicauli* floribus subsessilibus dif-  
fert.

*Typus*: Tharn Ngam Waterfall, Udon Thani,

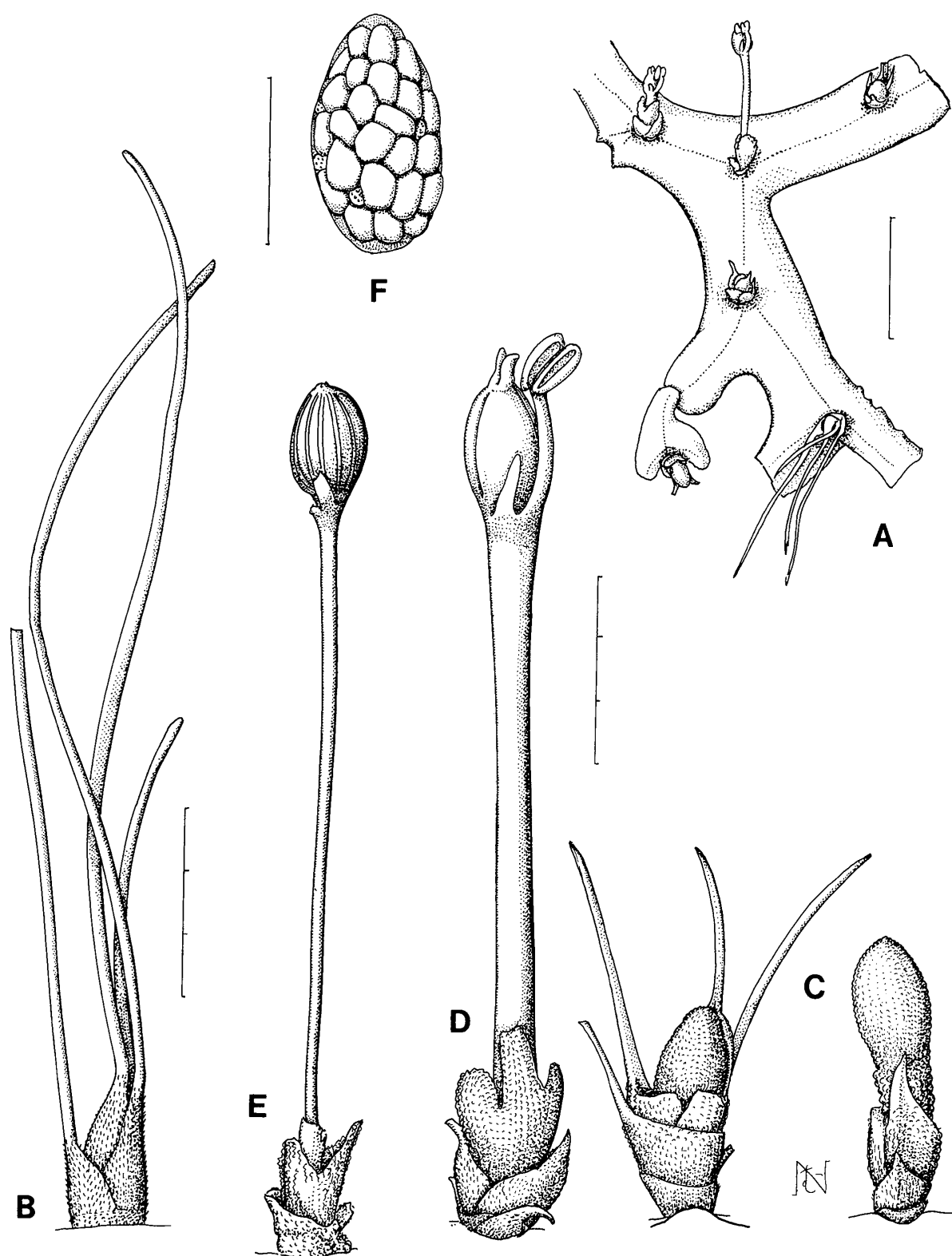


FIG. 20. *Polypleurum rubroradicans* (Kato et al. TL-708, type). A. Ribbon-like root with flowering shoots and tuft of leaves at branching points. B. Tuft of leaves with sheath-like bases. C. Flower buds covered by spathe-like bracts, which are acuminate (right) or needle-like (left). D. Flower at anthesis terminating peduncle above bracts. E. Stalked fruit. Note that outer tissues of peduncle are withered but not yet so at very basal portion. F. Ovules on ovary septum. Scale bars = 5 mm for A; 3 mm for B-E; 1 mm for F.

Northeastern Thailand, 17°09'N, 102°44'E, Feb. 27, 2003 (fr.), *M. Kato & T. Wongprasert TL-708* (holo BKF, iso TI, TNS).

Root ribbon-like, 3-5 mm wide, reddish purple when fresh, isotomously or anisotomously branched, with tufts of leaves on dorsal surface at all root branching points; leaves 4-6 per tuft, 7-13(-20) mm long, base sheath-like, deltoid-ovate, papillate, forming mound around leaves, distal part needle-like, caducous. Flowering shoots on dorsal surface at points of root branching; bracts 2-6, sheath-like, deltoid-ovate, papillate, acute or acuminate, 2-4 mm long, or distal part needle-like; flower terminal, 1, rarely with second lateral flower, bud covered by spathe, spathe papillate, ca. 3 mm long, ruptured into a few valves near apex at anthesis; peduncle 4-7 mm long or longer; tepals 2, 1 on each side of stamen, inserted at tip of peduncle, linear, narrowed to tip, 1-1.7 mm long; stamen 1, 2-2.3(-3) mm long, as tall as ovary or sometimes longer; ovary 2-locular, ellipsoid, slightly flattened, 1.8-2.3 mm long, 1.2-1.5 mm thick; stigmas 2, linear, narrowed to apex, 0.5-0.7 mm long, ovules on septum surface except on small lower central area (sometimes on whole surface), 14-22 per locule; capsule stalked (stalk 8-12 mm long), 1.8-2.3 mm long, 1.2-1.5 mm thick, asymmetric, ribs 10-12.

*Distribution:* Thailand (northeastern).

*Notes:* *Polypleurum rubroradicans* is similar to *P. longifolium*, *P. phuwaense* and *P. wongprasertii* in the sessile or subsessile flowering shoots, the papillate bracts and spathe, but differs from them in the wide, reddish purple roots. In the sessile or subsessile flowering shoots, it differs from *P. erectum* and *P. longicaule* with prominent flowering shoots. However, phylogenetically it is most closely related to *P. longicaule* (Y. Kita unpubl. data). *Polypleurum rubroradicans* differs from *P. wallichii* in having solitary stamens, and from it, *P. schmidtianum*, and *P. longistylusum* in the tufts of leaves and flowering shoots borne only at the

branching point of the roots.

## 20. *Polypleurum erectum* M. Kato, *sp. nov.* (Fig. 21)

A congeneribus surculis longis (usque ad 5 cm), erectis, foliis imbricatis, interdum plurifloribus dif-fert.

*Typus:* Cha Naen waterfall, Phu Wua Wildlife Sanctuary, Nong Khai, Northeastern Thailand, 18°14'N, 103°54'E, 150 m alt., 25 Feb. 2003 (fr.), *M. Kato & T. Wongprasert TL-706* (holo BKF, iso TI, TNS).

Root ribbon-like, 1-1.5 mm wide, isotomously or anisotomously branched, with shoots on dorsal surface only at all root branching points; vegetative shoot 1-5 mm long; leaves 5-10 per tuft, in 2 ranks, 15-30 mm long, base sheath-like, papillate, distal part needle-like. Flowering shoots also at root branching points, (5-)10-50 mm long, simple, occasionally with lateral flowers in addition to terminal flower; leaves (bracts) on flowering shoot many, in 2 ranks, imbricate, triangular, acute, acuminate or elongate needle-like, with sheath-like base, 2-5 mm long; peduncle 5-10 mm long or longer, flower bud covered by spathe, spathe papillate, ruptured near apex at anthesis, persistent, 5-7 mm long; tepals 2, 1 on each side of stamen, inserted at tip of peduncle, 1-1.5 mm long, narrowly deltoid, adnate to stamen at base; stamen 1, ca. 2 mm long, slightly longer than ovary, connective at middle of anthers; ovary 2-locular, asymmetric, ellipsoid, slightly flattened, 1-1.5 mm long; stigmas 2, conical, apex obtuse, 0.3-0.5 mm long; ovules covering entire septum surface except sometimes on small central area, 15-30 per locule; capsule stalked (stalk 12-20 mm long), 1.3-2 mm long, 0.9-1.1 mm thick, ellipsoid, asymmetric, ribs 10-13.

*Distribution:* Thailand (northeastern).

*Notes:* *Polypleurum erectum* is distinct from all other species of *Polypleurum* in the imbricate, leafy, long shoots and occasional lateral flowers, and, like



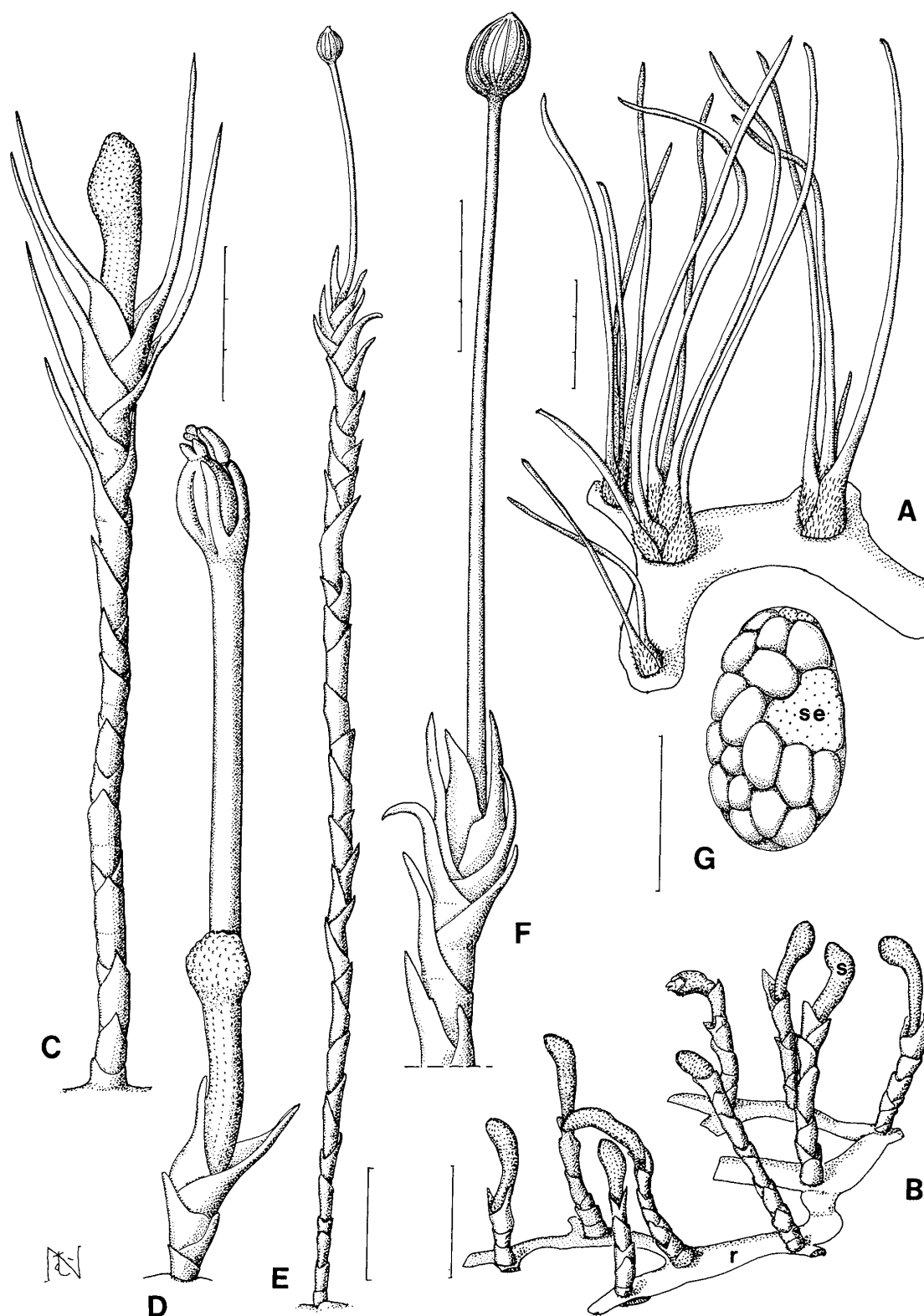


FIG. 21. *Polypleurum erectum* (A, M. Kato et al. 902; B-G, M. Kato et al. TL-706, type). A, B. Ribbon-like root (*r*) with tufts of leaves and with reproductive shoots bearing flower buds in spathe (*s*) at branching points. C. Shoot with many leaves and flower bud covered by spathe and subtended by terminal leaves. D. Flower at anthesis terminating peduncle on shoot. Note short shoot. E. Shoot with stalked fruit at apex. F. Stalked fruit at shoot apex (only distal part of shoot drawn). G. Ovules on ovary septum with sterile middle portion (*se*). Scale bars = 3 mm for A, C, D, F; 5 mm for B; 1 mm for E, G.

many other species, from *P. schmidtianum*, *P. wallichii* and *P. longistylosum* in the shoots (or tufts of leaves) being restricted to the root branching points. *Polypleurum erectum* is most closely related to *P. longifolium* (Y. Kita unpubl. data), but differs from it in the thinner root (1-1.5 mm vs. 2-3 mm in *P. longifolium*), shorter leaves (to 30 mm vs. to 40 mm), and the longer capsule stalk (12-20 mm vs. 4-7 mm).

*Other specimens examined:* Northeastern: Cha Naen waterfall, Phu Wua Wildlife Sanctuary, Nong Khai, st. Dec., fl. & fr. Jan., Somran Suddee 1767, M. Kato et al. TL-902, TL-903.

**21. *Polypleurum longicaule* M. Kato, sp. nov.**  
(Fig. 22)

A congeneribus surculis teretibus, crassibus (usque ad 2.5 mm), longissimis (usque ad 18 cm), ramificantibus, sparse foliatis subglabris, utrinque surculis brevibus floribus differt.

*Typus:* Tharn Ngam Waterfall, Udon Thani, Northeastern Thailand, 17°09'N, 102°44'E, 350 m alt., Dec. 21, 2003 (fr.), M. Kato, R. Imaichi, S. Koi & T. Wongprasert TL-1002 (holo BKF, iso TI, TNS).

Root green when fresh, ribbon-like, isotomously or anisotomously branched, to 2.5-4 mm wide, with leafy shoots on dorsal surface at all branch points; young shoots 0.5-2 cm long, ca. 1 mm thick, sparsely leafy, but densely leafy in apical portion, shoots floating, firm, green when fresh, terete, to 18 cm long, 2-2.5 mm thick, meandering, branched, with lateral branches alternate on both flanks, usually simple, 2-4 cm long, nearly glabrous; leaves on short young vegetative shoots many, in 2 ranks, 3-7 cm long, needle-like, those on long shoots sparse, caducous. Flowering shoots 1-3 cm long, on dorsal surface of root at branching points and on flanks of shoot; bracts 4-6, papillate at base, narrowly deltoid, acuminate, 2-4 mm long, ca. 1 mm wide at base or needle-like; flower 1, at apex of flowering shoot, rarely with additional lateral flower(s), bud cov-

ered by spathe, spathe 4-7 mm long, papillate, ruptured near apex at anthesis; peduncle 5-15 mm long; tepals 2, 1 on each side of stamen, inserted above base of stamen, linear, ca. 1 mm long; stamen 1, ca. 2 mm long, protruding from spathe, anthers slightly shorter than filament; ovary dark brown, ellipsoid, 1.6-2 mm long, ca. 1.2 mm thick, 2-locular (locules unequal); stigma ligulate, apex obtuse, ca. 0.7 mm long, branched at or above base; ovules on entire septum surface, 50-70 per locule; capsule stalked (stalk 5-20 mm long), ribs 12, valves unequal.

*Distribution:* Thailand (northeastern).

*Notes:* *Polypleurum longicaule* is characteristic in *Polypleurum* in the shoot being long, tough, floating in running water, nearly leafless (very sparsely leafy with leaves caducous?), and branched, and is similar to *Diplobryum koyamae* and *D. ramosum* in this character, if the branched axis of the latter species is a shoot (Kato & Fukuoka 2002). The species of *Diplobryum*, however, are characterized by the 20-ribbed capsules, the tepals and stamen inserted near the middle of the ovary stalk (to 5 mm long vs. inserted at the tip of the long peduncle in *P. longicaule*), and 2 stamens with biforked filaments. In the prominent shoot it is also similar to *P. erectum*, but the mature shoot is nearly glabrous, much longer and branched. *Polypleurum longicaule* is most closely related to *P. rubroradicans* and not to *P. erectum* among the species examined (Y. Kita unpubl. data). The phylogenetic relationships of *D. koyamae* and *D. ramosa* are not known.

*Other specimens examined:* Northeastern: Tharn Ngam Waterfall, Udon Thani, st. Jul., fl. Jan., fr. Feb., Somran Suddee 1779, M. Kato & T. Wongprasert TL-709, M. Kato et al. TL-901.

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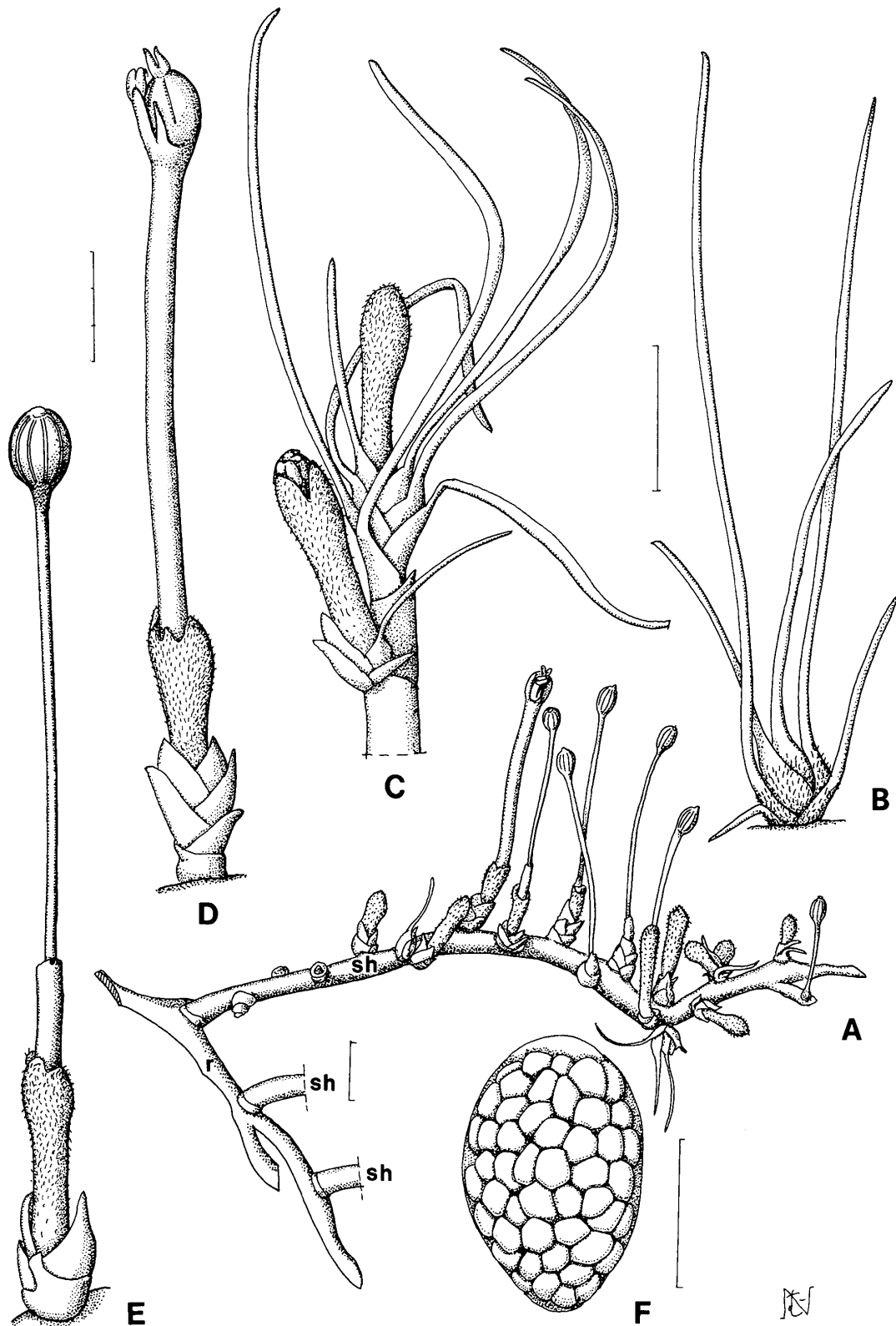


FIG. 22. *Polypleurum longicaule* (Kato et al. TL-1002, type). A. Shoots (*sh*; two of three cut above base) arising from root (*r*) and bearing flowering shoots. B. Tuft of leaves with sheath-like base. C. Terminal and lateral flower buds covered by spathe (basal part of shoot not drawn). D. Young pedunculate flower on shoot. E. Fruit on shoot. Note that outer tissues of peduncle are withered at this stage, but not yet so at basal portion (see also A). F. Ovules on ovary septum. Scales bars = 5 mm for A, B; 3 mm for C-E; 1 mm for F.

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**Appendix.** Nomenclatural changes for non-Thai species of Podostemaceae in relation to the present treatment of Podostemaceae of Thailand.

**1. *Cussetia carinata*** (Lecomte) M. Kato, comb. nov. — *Terniola carinata* Lecomte, Bull. Soc. Bot. Fr. 56: 96, 1909; Fl. Gén. Indochin. 5: 45, f. 5A, B, 1-4, 1926 — *Lawia carinata* (Lecomte) Koidz., in Doi, Fl. Satsum. 1(4): 53, 1929 — *Dalzellia carinata* (Lecomte) C. Cusset, Fl. Cambodge, Laos, Viêt-Nam 14: 78, pl. 12, f. 4-7, 1973; Cusset & Cusset, Bull. Mus. Natl. Hist. Nat. Paris, 4<sup>e</sup> sér., sect. B, Adansonia 10(2): 173, 1988. *Typus*: Cambodia, 1874, *Julien s.n.* (P!).

*Distribution*: Cambodia, Laos.

**2. *Terniopsis australis*** (C. Cusset & G. Cusset) M. Kato, comb. nov. — *Tristicha australis* C. Cusset & G. Cusset, Bull. Mus. Natl. Hist. Nat. 4<sup>e</sup> sér. Sect. B, Adansonia 10: 171, 1988 — *Malaccotristicha australis* (C. Cusset & G. Cusset) M. Kato, Y. Kita & Koi, Aust. Syst. Bot. 16: 179, f. 2-3, 2003. *Typus*: Katherine Gorge, Northern Territory, Australia, *N. Byrnes* 2343 (holo MEL; iso BRI, CANB, NT!, NSW!).

*Tristicha trifaria* auct. (non Sprengel); Aston, Aquat. Pl. Aust. 148, f. 57, 1973, p.p.; Fl. Aust. 18: 3, f. 17E-G, 1990, p.p.

*Distribution*. Australia (Northern Territory, Western Australia).

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